University of Alberta

Genetic variation studies in *Pterocarpus macrocarpus* Kurz as revealed by isozyme, morphological and physiological traits

by

Chaiyasit Liengsiri

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Genetic variation studies in *Pterocarpus macrocarpus* Kurz as revealed by isozyme, morphological and physiological traits submitted by Chaiyasit Liengsiri in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

Genetic variation among populations and families within population was revealed in natural populations of *Pterocarpus macrocarpus* Kurz in Thailand by isozyme analysis and by evaluation of seedling growth, morphology and physiological traits.

Isozyme analysis of 18 loci revealed a high level of genetic variability within and among 11 populations. On average, each population was polymorphic at 82.32% of the loci and number of alleles per locus was 2.67. Observed and expected heterozygosities were 0.222 and 0.246, respectively. All loci exhibited allelic frequency heterogeneity among populations and the estimate of F_{ST} was 0.121. There was an east-west pattern of population differentiation. Genetic distance correlated with geographic distance of populations ($r = 0.515$; $P < 0.0001$), suggesting that isolation by distance might have contributed to population differentiation.

Outcrossing rates varied among populations from 0.620 to 0.931 for single-locus and from 0.719 to 0.959 for multilocus. The lower estimates in eastern populations might be due to habitat characteristics, degree of disturbance, density, and distribution of flowering mature trees. Among-tree variation in outcrossing showed that reduced density associated with disturbance could result in low outcrossing in some eastern populations.

Populations accounted for 9-18%, 3-5% and 16-21% of the phenotypic variation in height, diameter and biomass traits, respectively. The corresponding percentage estimate due to families within population was 13-31%, 16-21% and 3-15%. Heritability estimates ranged from 0.39±0.07 to 1.00±0.11 for individual trees and from 0.69±0.04 to 0.90±0.02 for families. Genetic correlation estimates among height, diameter and

biomass traits ranged from –0.12±0.13 for shoot-to-root ratio and 3-week height to 0.89±0.34 for stem dry weight and 18-week height.

Among physiological traits, only water-use efficiency (WUE) exhibited significant population differentiation, but could account for only 2% of total phenotypic variation. Families within populations were significant, accounting for 13%, 13% and 7% of the phenotypic variation in net photosynthesis (*A*), transpiration (*E*) and WUE, respectively. Estimates of individual heritability were 0.40±0.09 for *A*, 0.43±0.09 for *E* and 0.26±0.08 for WUE. The corresponding family estimates were 0.60±0.08, 0.62±0.07 and 0.47±0.10. Transpiration correlated strongly with *A* (0.78±0.12) but negatively with WUE (–0.48±0.18). Net photosynthesis did not correlate genetically with WUE. The estimates of genetic correlation with 26 growth traits were low. However, 11 of 26 estimates for WUE were ≥ 0.2 and the range was from 0.20±0.16 with tap root dry weight to 0.32±0.16 with 30-week height.

During period of water stress treatment significant differences in *A*, *E*, WUE, and xylem water potential were apparent among populations and families within population. Water stress preconditioning improved the ability of seedling in drought tolerance.

This dissertation is truly dedicated to my parents. My late father, Kokjeng Saelim, and my dearest mother, Tuajia Saetang, both have inspired, encouraged and persistently supported my academic pursuit since my childhood.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

1.1 Introduction

The decline and loss of the forested portion of the globe has been vast and has caused grave concern among scientists and policymakers worldwide (Anonymous 1991). FAO (1997) has estimated that at the close of the twentieth century, there are approximately 3,500 million hectares of forests in the world, with 1,500 million hectares found in the developed countries and 2,000 million hectares in developing countries. Almost all the losses in forested areas are a direct consequence of human intervention. Although losses have also occurred in temperate forests, currently the greater concern is about the losses in the tropical forests which have been estimated to be home to at least two-third of the world's organisms (Raven 1986; Anonymous 1991). Deforestation is recognised as the major cause of the destruction of the tropical forests and the loss of biodiversity. FAO (1997) has estimated the annual rates of deforestation in developing tropical countries at 15.5 million hectares for the period 1980-1990 and 13.7 million hectares for the period 1990-1995. It is estimated that the total of 200 million hectares of tropical forests has been lost to deforestation during 1980-1995.

Deforestation may lead to the loss or the extinction of local populations of some species as well as a reduction in the size of remnant populations (Bawa 1994). Both deforestation and forest fragmentation could result in change in pattern of genetic diversity (variation) within forest species. Some rare alleles may be lost due to fragmentation but most genetic diversity will not be lost immediately. The rate and

severity of genetic diversity loss will depend on several factors, such as magnitude and frequency of forest destruction, degree of isolation among fragmented forests (Bawa 1994). Genetic diversity is the basis for the natural evolution and adaptation of species to new, changing environments. Even if forests are regenerated by natural or artificial means, they may become less capable of genetic adaptation to environmental challenges and to future large-scale stress (Anonymous 1991). Forest management practices also affect genetic diversity (Savolainen and Kärrkkäinen 1992; El-Kassaby and Namkoong 1994). Harvesting may lead to a reduction in stand density, which may result in an increase in the level of inbreeding (Murawski and Hamrick 1992) and a subsequent decline in genotypic diversity. Murawski et al. (1994a) found that logged stands of *Shorea megistophylla* show a higher level of inbreeding than stands that have not been logged. Selective felling of large and superior individuals, which is commonly practised over extensive areas of indigenous tropical forests, may also lead to dysgenic selection (Bawa 1994).

Deforestation is a serious problem of Thailand. In 1985, Thailand had 150,866 km^2 (approximately 15 million hectares) of forested areas which accounted for 29% of the total area, and by 1995 the forests has declined to 131,485 km^2 (approximately 13 million hectares) which is 25% of the total area (Royal Forest Department 1997). It is estimated that the annual loss of forests in Thailand is 330,000 hectares (FAO 1997). The major causes of deforestation are due to (1) rural proverty and population growth which increase the demand on agricultural land and forest products, and (2) the improvement of the country's physical infrastructure, such as road and dam construction, etc. (Boontawee et al. 1995). Despite a shift in government policy on environmental conservation, the rate

of forest degradation and deforestation is still high. The result of these problems is that much of forest biodiversity, in terms of habitat, forest ecosystem, species, population and genetic diversities, seems to be endangered (Boontawee et al. 1995).

Pterocarpus macrocarpus Kurz is a commercially valuable timber tree not only in Thailand but also in the international timber trade (Anonymous 1979). Prior to the logging ban in 1988, *P. macrocarpus* was the second most valuable timber species after teak (*Tectona grandis*), in terms of export earnings. In 1988, timber of *P. macrocarpus* earned over 11 million US dollars (Royal Forest Department 1989). In northeastern Thailand, *P. macrocarpus* is one of the species planted by rice farmers, who consider it to be fast growing and valuable for construction and fuel (Rathket 1989). Recently, the Royal Forest Department identified *P. macrocarpus* as an important plantation and agroforestry species.

Despite its economic and ecological importance there has been little effort to investigate its biology, ecology and genetics, and to develop a management strategy that is required for maintaining a stable productive and sustainable resource. Although over the past few years *P. macrocarpus* has become an important species for much of the research conducted in Thailand, knowledge about the biology of the species remains limited. Liengsiri (1997) studied flowering phenology of this species. A series of four progeny-provenance trials including 90 families from nine provenances were planted in 1995 by ASEAN Forest Tree Seed Centre Project, Thailand. However, these trials are still too young to provide useful information. Piewluang et al. (1997) studied variation in fruit and seed size and quality within and among natural populations of *P. macrocarpus*. They observed significant variation within and among populations and between years for

all fruit and seed traits. Chaisurisri et al. (1998) studied provenance level variation in gas exchange parameters (i.e., photosynthesis, transpiration and water-use efficiency). They also found significant differences among *P. macrocarpus* provenances in gas exchange parameters, although these differences represented only three percent of the total variation indicating a relatively small amount of genetic variation in these gas exchange traits.

Although a ban on logging in the country has been implemented since 1988, *P. macrocarpus* is still logged illegally. The rapid depletion and exploitation of forest resources could cause a serious erosion of genetic resources in *P. macrocarpus*. The problem becomes more pronounced with the increasing demands on agricultural lands and forest products. In order to maintain the potential and opportunity for species evolution, genetic improvement, resource management and conservation, it is important to understand the amount and distribution of genetic variation in the species. A genetic study of *P. macrocarpus* is therefore an important priority. It provides essential knowledge required to design and develop effective sampling and management strategies for sustainable utilization and conservation of genetic resources of *P. macrocarpus*. Genetic variation can be assessed using biochemical markers, molecular markers, morphological traits, and physiological parameters. However, these different approaches may reveal different or similar pattern of genetic variation for a species. Biochemical markers, such as isozymes, are useful for monitoring broad changes in genetic diversity but may or may not be indicative for selective advantage or disadvantage. On the other hand, quantitative traits are adaptive traits that contribute to the fitness of plants. Therefore, it is of utmost importance to conduct complementary studies of genetic variation using different approaches. The combined knowledge will allow the better

understanding of evolutionary forces which will be very useful for the meaningful development of management and conservation strategies of genetic resources of the species.

In this thesis, genetic variation in *P. macrocarpus* has been studied on materials obtained from Thailand, using isozyme markers, morphological traits of seedling growth, and physiological (gas exchange) parameters measured from seedlings. The objectives are:

1. to determine the amount and distribution of genetic variation in natural populations of *P. macrocarpus*,

2. to investigate the mating system in natural populations of different degrees of habitat disturbance,

3. to determine the magnitude of genetic variation, genetic control and genetic relationship in morphological and physiological traits of seedlings grown in the nursery,

4. to investigate the pattern of gas exchange and water relations in response to water stress of seedlings under nursery conditions, and

5. to develop strategies for genetic resource management and conservation of *P. macrocarpus*.

1.2 Literature review

1.2.1 Biology of *Pterocarpus macrocarpus* Kurz

The genus '*Pterocarpus*' belongs to the subfamily Papilionaceae of the family Leguminosae. It is a pantropical genus consisting of 20 species; 11 in tropical western Africa, 5 in the Indo-Pacific region and 4 in tropical south America (PROSEA 1994).

Pterocarpus produces beautiful, highly decorative timber that ranks among the finest luxury woods in the world (Anonymous 1979).

Pterocarpus macrocarpus Kurz is one of the most important commercial tree species of mainland southeast Asia. The tree is indigenous to Burma, Thailand, Laos, Cambodia and Vietnam (Rojo 1977). *P. macrocarpus* has a variety of common names in the countries in which it occurs, including *paduak* (Burma), *pradu* (Thailand), *mai dou* (Laos), *thnong krop thom* (Cambodia), and *giang huong trai to* (Vietnam) (Troup 1921; Smitinand 1980).

P. macrocarpus is not a gregarious tree, but grows scattered and in association with other species. It can be found in mixed deciduous forest and dry dipterocarp forest at an altitude between 100 to 600 m (Santisuk and Niyomthamma 1983). Although unusual occurring, it can be found in hill evergreen forest along the edge of forest transition zone from dry dipterocarp forest (Liengsiri, personal observation). In mixed deciduous forest, it occurs in association with *Tectona grandis*, *Xylia xylocarpa*, *Afzelia xylocarpa*, *Largerstroemia calyculata*, *Terminalia alata*, *Vitex pinnata* and bamboos (Bunyavejchewin 1983). In the dry dipterocarp forest, it occurs in association with *Shorea obtusa*, *S. siamensis*, *Dipterocarpus obtusifolius*, *D. tuberculatus*, *D. intricatus*, *Xylia xylocarpa*, *Canarium subulatum*, *Careya sphaerica*, *Melanorrhoea usitata*, *Quercus kerrii* and *Aporusa villosa* (Komkris 1965). It tolerates a wide range of temperature and rainfall conditions within its natural range. Mean maximum temperatures of 37.7-44.4°C and mean minimum temperatures of 4.4-11.1°C can be tolerated. Average annual rainfall varies from 889 to 3,572 mm (Chanpaisang et al. 1994).

P. macrocarpus is a medium to large deciduous forest tree; growing to 30 m with a girth of 3.5 m but ordinarily attaining a height of 15 to 20 m with a clear bole of 6 to 12 m and a girth of 1.3 to 2 m (Troup 1921). The bark is greyish brown to dark brown with irregular exfoliated scales. When cut, the bark exudes a bright red resin. The leaves are imparipinnate compound, 15 to 23 cm long, with 5 to 10 leaflets arranged sub-opposite to alternate in 3 to 5 pairs with one terminal leaflet. The leaflets are 3 to 6 cm long, ovate to oblong with a rusty, faintly pubescent 1 cm long petiole. The tree is leafless during the dry season (December to March) (Santisuk and Niyomthamma 1983).

P. macrocarpus is an entomophilous hermaphroditic species with a perfect, yellow flower blooming from March to May (Santisuk and Niyomthamma 1983). The inflorescence is an indeterminate raceme; flowers develop acropetally, i.e., flowers in the proximal portion of the inflorescence bloom first while those in the distal portion are in the early stage of development. Individual inflorescences at the full development stage are 5 to 15 cm long and have 20 to 40 flowers (Liengsiri 1997). Anthesis (blooming) for a single flower is short. The flower opens in the early morning and appears receptive for about 6 hours. Abscission of unpollinated flowers occurs in the afternoon of the same day. The flowering episode within an individual tree can last 2 to 3 weeks (Liengsiri 1997).

Fruits develop during the rainy season from May through September and mature in October and November. The entire reproductive cycle from pollination to fruit maturity takes about 8 months (Ram-in and Owens, unpublished data). The fruit is a compressed, indehiscent samara, disk-like, broadly winged with a thickened woody or corky central portion bearing 1-3 seeds (Troup 1921). The seed is kidney-shaped, with a smooth to

undulating, brown to blackish seedcoat (PROSEA 1994). Germination is epigeous. The radicle issues from the side of the fruit opposite the stalk, bending downwards into the ground. The cotyledons are extricated by the arching of the hypocotyl (Troup 1921). The optimal range of temperatures for germination is 25-35°C (Liengsiri 1987).

The wood is of medium weight, moderately hard to hard, very strong and durable. Wood density at 12% MC is 920 kg/m^3 and the durability in contact with the ground varies from 5 to 18 years (Tonanon 1985). The yellowish red to brick red wood is fine to moderately fine grained, easy to work and plane, sands and finishes well. The wood is used for light to heavy construction, floors, pillars, posts, joists, beams, furniture, shafts of carriages and agricultural implements (Santisuk and Niyomthamma 1983).

1.2.2 Genetic variation studies

Genetic diversity (variation) is the mainstay of biological stability which enables species to adapt to changing environments and to survive (Anonymous 1991). Genetic variation is a result of changing evolutionary histories and in itself is of value to the present and future individuals, populations and species in which it occurs (Namkoong 1992). Therefore, information on genetic variation of forest tree species is fundamental to genetic management and conservation (Ericksson et al. 1995). Selection, mutation, random genetic drift, migration and mating systems are among the most important evolutionary determinants of genetic variation (Hartl and Clark 1989). However, current human activities and impacts, such as deforestation, air pollution, forest management, etc., on forest resources appear to outpace evolutionary forces in altering and shaping the genetic variation of natural forest resources (Lande 1988). Maintaining genetic diversity

is crucial to preserve the evolutionary potential of species (Hamrick et al. 1991). Knowledge of the levels and distribution of genetic variation thus becomes a prerequisite for effective and efficient forest management and conservation programs (Savolainen and Kärkkäinen 1992; Yang and Yeh 1992; El-Kassaby and Namkoong 1994). Genetic variation can be assessed in several methods, such as morphological traits, physiological traits, biochemical markers (terpene, isozyme) and DNA.

1.2.2.1 Isozyme variation

Over the past several decades, isozymes as genetic markers have been widely used to investigate the pattern of genetic variation in plant species (e.g., Conkle 1971; Brown 1979; Ledig 1986; Hamrick and Godt 1990; Kertadikara and Prat 1995; Jaquish and El-Kassaby 1998). Isozyme markers represent electrophoretically detectable forms of enzymatic proteins visualized by substrate-specific staining (Ayala 1982). Isozymes enable the study of many loci and individuals simultaneously. The predominantly codominant expression of enzyme variation, absence of environmental effects (Lewontin 1974), low cost and technical simplicity of the analysis (Wendel and Weeden 1989) are among the main reasons for the widespread use of isozymes as genetic markers in the study of genetic variation.

The levels of genetic variation vary among plant species and there are differences within and among populations as well (Hamrick et al. 1992; Moran 1992). Life history and ecological characteristics have been cited as factors influencing levels of genetic variation in plant species (Hamrick and Godt 1990; Hamrick et al. 1992). These characteristics include taxonomic status, regional distribution, geographic range, life

form, mode of reproduction, breeding system, seed dispersal mechanism and successional status (Hamrick and Godt 1990). Thus species' traits have different degrees of influence on species' genetic diversity. Generally, species with large geographic ranges, that are long-lived, wind-pollinated and have outcrossing breeding system, and wind or animal-ingested seed dispersal maintain more genetic variation within species and populations than do species with other combinations of traits. Species with this particular suite of traits also have a lower proportion of their genetic diversity among populations (Hamrick and Godt 1990; Hamrick et al. 1992).

Genetic diversity within populations is a function of the amount of genetic diversity present in the species and the partitioning of this variation among populations. Two factors having the greatest influence on genetic diversity within population level are geographic range and genetic mobility (Hamrick et al. 1991). Generally the most common measures of genetic diversity within a population are percentage of polymorphic loci (P), average number of alleles per locus (A), the number of alleles per polymorphic locus (AP), observed heterozygosity (H_O) and expected heterozygosity (H_E) in a random breeding population. In general, forest trees are highly variable genetically (Hamrick 1994).

Forest tree species are long-lived organisms with widespread distribution, high fecundity and a predominantly outcrossing mode of mating system, and thus maintain high levels of genetic variation within populations and low levels of genetic differentiation among populations (Hamrick 1979; Yeh 1989). In conifers, the general findings indicate moderate to high levels of genetic diversity in most forest tree species (H_E = 0.171, Hamrick 1994). However, low levels of genetic diversity were also observed

in some species, such as *Pinus resinosa* (Fowler and Morris 1977), *Thuja plicata* (Yeh 1988). In tropical forests, low population density and the speculation of self-fertilization as the predominant breeding system led to the early hypothesis that most tropical species would have relatively low genetic diversity (Fedorov 1966). Current evidence from isozyme data, however, indicates that tropical species also have high levels of genetic variation (Hamrick and Godt 1990; Loveless 1992). The level of genetic diversity (H_E = 0.160) of tropical species is comparable to that of temperate conifers (H_E = 0.171) (Hamrick 1994). The majority of tropical species are obligately outcrossed by virtue of being either self-incompatible or dioecious (Bawa 1974; Chan 1981; Bawa et al. 1985). There is evidence that pollen movement over distances of several kilometers may be common in the tropics (Hamrick and Loveless 1989; Hamrick and Murawski 1990; Nason et al. 1996). In the study of pollen movement in some species of *Figus*, which were pollinated by species-specific wasps, Nason and Hamrick (1997) found these highly coevolved pollinators to be efficient agents of long-distance pollen dispersal, routinely dispersing 6-14 km between flowering trees. Thus, being outcrossing species with extensive gene flow is attributable to the high levels of genetic variation in most tropical species (Bawa 1994).

Levels of genetic differentiation among populations are commonly measured using *F*-statistics (F_{ST}) of Wright (1965) or *G*-statistics (G_{ST}) of Nei (1973). F_{ST} is the correlation between random gametes within a population with gametes in the total of all populations while G_{ST} is the measure of the genetic differentiation among populations relative to total variation. Forest tree species also differ greatly with respect to genetic divergence among populations. The geographical range of species seems to have

significant effects on the level of genetic differentiation among populations (Hamrick 1983; Joly et al. 1992). Regional and localized species also tend to exhibit greater differentiation among populations than widespread species (Moran et al. 1989; Xie et al. 1992). In conifers, the levels of genetic differentiation among populations as estimated from G_{ST} values vary from 1% (G_{ST} = 0.01) for *Picea mariana* (Boyle 1985) to 30% (G_{ST} = 0.30) for *Pinus halepensis* (Berg and Hamrick 1997).

Levels of population differentiation in tropical species as revealed by G_{ST} values also vary from 0.038 for *Casuarina cunninghamiana* (Moore and Moran 1989) to 0.219 for *Pentaclethra macroloba* (Bawa 1994). Generally, there is more population differentiation in tropical tree species (averaged G_{ST} = 0.135) than in temperate tree species (averaged G_{ST} = 0.099) (Hamrick 1994). Lower population densities, more widely scattered populations that reduce gene flow and increase genetic drift, and greater spatial variation in the natural selection pressure are among the factors attributable to higher level of population differentiation in tropical species (Bawa 1976). The mode of pollen and seed dispersal also influences genetic differentiation, since wind-pollinated species exhibit less among-population genetic differentiation than animal-pollinated species (Loveless and Hamrick 1987).

Forest tree species maintain high levels of genetic diversity. Generally, a large proportion of the genetic variation of forest tree species resides within populations while genetic variation among populations accounts for only a small portion of the total genetic variation. Millar and Libby (1991) grouped forest tree species into several classes according to their unique genetic profile, which defines their hierarchical structure of variation. These classes include species with (1) little or no genetic variation within

populations, (2) no variation within but variation among populations, (3) little variation within populations and little variation among populations, (4) high variation within populations, combined with little variation among populations, and (5) high variation within populations together with high variation among populations. Understanding the pattern and distribution of genetic variation in a species, therefore, is essential for effective management, utilisation and conservation of forest genetic resources, because a genetically effective management strategy for one species may not be effective for another (Hamrick et al. 1991).

1.2.2.2 Mating systems

The mating system determines the pattern in which gametes unite (Allard et al. 1975); it governs the frequency distribution of genotypes in populations. Recently, isozyme data have facilitated the study of mating systems in plant species (e.g., Brown et al. 1975; Cheliak et al. 1985; Murawski et al. 1994b). Outcrossing rate (t) is the parameter most commonly used to described the mating system. Outcrossing refers to the mating of genetically nonidentical individuals (Brown et al. 1975). Outcrossing rates can vary from 0 to 1, where a value of 0 indicates 0% outcrossing (no outcrossing) and a value of 1 indicates 100% outcrossing. Estimates of outcrossing rates can be based on a single locus and multiple loci (Brown et al. 1975; Ritland and Jain 1981).

Most forest trees are outcrossing species. Yeh (1989) listed published reports of outcrossing rates in conifers ranging from 0.88 in *Pinus banksiana* (Cheliak et al. 1985) to 0.98 in *Picea glauca* (Cheliak et al. 1984). Tropical trees are also largely outcrossed and the estimates of outcrossing rates are generally greater than 0.80 (see review in Nason

and Hamrick 1997). However, some tropical tree species have low outcrossing rates, such as *Cavanillesia plantanifolia*, which has outcrossing rates ranging from 0.213 to 0.661 (Murawski and Hamrick 1992).

Outcrossing rates may vary between populations within a species (Brown et al. 1975), although in some species they may not vary greatly among populations (Boyle and Morgenstern 1986). Boyle et al. (1992) estimated outcrossing rates of *Pinus kesiya* ranging from 0.68 to 0.97 among four populations from northern Thailand.

In addition, variation in outcrossing rates among individual trees within a population also occurs in some species. For instance, Murawski et al. (1994b) observed tree-to-tree variation in outcrossing rates in *Shorea congestiflora* and *S. trapezifolia*, two endemic tropical tree species from Sri Lanka. In *S. congestiflora*, outcrossing rates vary from 0.4 to 1.0 with the majority of trees having outcrossing rates greater than 0.8. In *S. trapezifolia*, however, outcrossing rates among trees ranged from 0.0 to 1.0, although the majority of trees had outcrossing rates of greater than 0.8. Apart from tree-to-tree variation, *S. trapezifolia* also displayed a year-to-year variation in outcrossing rates as well (Murawski et al. 1994b). Eight trees had outcrossing rates that ranged from 0% to 20% in 1990, while in 1991 only three trees had such low outcrossing rates, although the total number of trees sampled in both years was more or less the same. Differences in genetic compositions and environmental conditions (Clegg 1980), stand density (Murawski and Hamrick 1992), phenological variation (Hall et al. 1994), availability and foraging behavior of pollinators (Cruzan et al. 1994) are among the factors that can affect the variation in outcrossing rates. Because the mating system plays an important role in determining subsequent population structure and the dynamics of variation over

generations (El-Kassaby and Namkoong 1994), detailed information on the mating system is important to design proper management strategies for genetic improvement and conservation.

1.2.2.3 Morphological variation

Most genetic variation studies in forest trees in the last 20 years have measured isozyme variation (e.g., Feret 1971; Cheliak et al. 1984; Hamrick et al. 1992; Jaquish and El-Kassaby 1998). Although isozyme markers are useful for monitoring broad changes in genetic diversity or levels of inbreeding, changes of adaptive characters, however, are likely to go undetected because of the low correlation in level and pattern of variation between isozymes and adaptive characters (Savolainen and Kärkkäinen 1992). Hattemer (1991) also pointed out that patterns of variation at selected loci may differ from that of neutral loci. This limits the usefulness of isozyme markers in monitoring important genetic changes. Thus, complementary studies on variation in morphological traits that are known to contribute to the adaptive significance or fitness of plants are needed.

Individual plants may respond to the environment by altering their morphological characteristics. This ability is referred to as phenotypic plasticity (Bradshaw 1965), which is considered adaptive if plant fitness is enhanced (Schlichting 1986). The plasticity of a characteristic is itself under genetic control and modified by selection (Bradshaw 1965; Khan and Bradshaw 1976). Most morphological characteristics are controlled by several or many gene loci, each of which is assumed to have a relatively small effect on the phenotype (Zobel and Talbert 1984). An important aspect of this type of inheritance is that individuals cannot generally be placed into distinct groups. These traits, which

exhibit continuous variation, are called quantitative traits or metric traits, and their study depends on measurement instead of counting (Zobel and Talbert 1984). In plants, studies of genetic variation in quantitative traits (e.g., height, diameter, yield) involve observations of variation in performance of a large number of samples or progenies of different parents planted under uniform environmental conditions (common garden) on one or more planting sites. These studies can, however, be expensive and time-consuming, because many quantitative traits are expressed only after several years of growth. In addition, quantitative traits are also affected by environmental factors (Hamrick et al. 1992).

The concept of heritability is one of the most important and most commonly used genetic parameters in the studies of variation in morphological traits. Heritability values express the proportion of variation in the population that is attributable to genetic differences among individuals (Zobel and Talbert 1984). It is, therefore, a ratio determining the degree of resemblance between relatives. There are two types of heritability estimates, broad-sense and narrow-sense. Broad-sense heritability is defined as the ratio of total genetic variation in a population to phenotypic variation, whereas narrow-sense heritability is the ratio of additive genetic variance to total variance (Zobel and Talbert 1984). Both broad-sense and narrow-sense heritabilities can range from 0 to 1. A lower limit of 0 indicates none of the variation in a population is attributable to genetics while the upper limit of 1 indicates all variation is due to genetic effects. Most heritability estimates in forest genetics are for narrow-sense heritability, because most tree improvement programs are aimed at improving general combining ability and thus utilize only the additive portion of the genetic variance.

An important aspect of heritability estimates is that they apply only to a particular population growing in a particular environment at a particular time; thus heritability is not a fixed value for a given trait of a species (Zobel and Talbert 1984). Change of heritability or genetic control with age has been observed (e.g., Namkoong and Conkle 1976; Franklin 1979). Heritability estimates also vary among traits. Cornelius (1994) compiled, from 67 published reports, heritability estimates of seven traits. He reported that heritability of wood specific gravity was almost always above 0.3, while heritabilities for other traits tended to be low and ranged from 0.18 to 0.26. However, Wu et al. (1995) reported higher heritability estimates in *Pinus contorta*, ranging from 0.43 to 0.71 for traits of absolute height and diameter. Therefore, heritability is only a relative indication of genetic control and should not be interpreted as absolute or invariant value (Zobel and Talbert 1984).

In addition to heritability, genetic correlation among traits is also an important genetic parameter. Different traits may be correlated because they are influenced in part by genes which affect both traits or because they are influenced by different genes that are linked on the same chromosome (Baker 1986). Genetic correlation is used mainly for four different purposes (Williams and Matheson 1994): (1) to predict response at harvest to selection carried out in young trees, (2) to predict response in a trait that is hard to measure from one which is easy to measure, (3) to predict response to selection at one site when selecting at another, and (4) to be used in association with heritability to construct selection indices. Forest trees are typical of long rotations and delayed reproductive maturity and, therefore, long breeding cycles. Maximizing genetic gain per unit time is the ultimate objective of all applied tree improvement programs (Zobel and Talbert

1984). The use of genetic correlation to help make selections at early ages has been widely investigated and is a common practice used to shorten breeding cycles in advance generation tree improvement programs (e.g., Lambeth 1980; Foster 1986; Wu et al. 1995; Xie and Ying 1996).

1.2.2.4 Physiological variation

Physiological processes reflect the interaction between the genotype and the environment, because physiological processes are the machinery through which the genetic potential and the environment operate to determine the quantity and quality of growth (Kramer 1986). Most physiological processes are complex and sensitive to the environments (Mahon 1983). Thus, actual productivity usually is far below the genetic and physiological potential because of inhibition of environmental stresses to important physiological processes (Kramer 1986). The study of physiological processes, therefore, provides information on the relationship between physiological processes and the inhibitory effects of environmental stresses. The understanding of this relationship would enable tree breeders to identify the physiological limitations to growth and to find ways to increase forest productivity (Kramer 1986).

Photosynthesis determines growth rate and yield and thus has been extensively studied (Nelson 1988). Currently, genetic variation in photosynthesis has been investigated in several forest tree species, for instance, *Pinus ponderosa* (Monson and Grant 1989), *Picea abies* (Larsen and Wellendorf 1990), *Acacia auriculiformis* (Cole et al. 1994), *Eucalyptus camaldulensis* (Gibson et al. 1995). Boltz et al. (1986) observed differences in photosynthesis among loblolly pine (*Pinus taeda*) seedlings from six

widely separated provenances. They also observed the seasonal patterns of net photosynthesis which peaked in late growth season. Dunlap et al. (1993) found that black cottonwood (*Populus trichocarpa*) clones from xeric regions had higher photosynthetic rates than those from mesic regions when grown under a summer climate. Cregg (1993), however, found no seed-source differences in photosynthesis among mature ponderosa pine trees. Similarly, Sulzer et al. (1993) did not observe differences in photosynthesis among families of black spruce (*Picea mariana*) seedlings. Mebrahtu and Hanover (1991), however, observed significant family variation in net photosynthetic rate in black locust (*Robinia pseudoacacia*) seedlings.

Because photosynthesis provides most of the materials used in growth, it is often assumed that an increase in the rate of photosynthesis should result in an increase in growth (Zelitch 1975). However, attempts to correlate growth and yield with rates of photosynthesis have been disappointing (Nelson 1988). The relationship between photosynthesis and growth and yield may be positive (Ceulemans et al. 1987; Blake and Yeatman 1989; Mebrahtu and Hanover 1991), negative or nonexistent (Nelson 1988; Larsen and Wellendorf 1990). There are many possible factors that may partially explain such variation or lack of correlation. Total dry matter production depends not only on the rate of photosynthesis per unit of leaf area but on total leaf area, leaf duration and canopy exposure (Kramer 1986). Photosynthetic rate generally changes during the growing season (Boltz et al. 1986; Blake and Yeatman 1989). Photosynthetic rate also depends on the environment in which plants are raised (Hutchison et al. 1990); morphological structure can also influence the rate (Mahon 1983). The amount of wood produced also depends on how much photosynthate is used in respiration and how the remainder is

partitioned among the various organs of the tree (Kramer 1986; Nelson 1988). Despite the inconsistent results between photosynthesis and yield, photosynthesis has been suggested as an early selection criterion to improve the efficiency of tree breeding (Lapido et al. 1984; Ceulemans et al. 1987; Larsen and Wellendorf 1990).

Photosynthesis and transpiration are intrinsically intercorrelated (Dang et al. 1994); therefore, one of the inevitable consequences of photosynthetic CO_2 uptake through the stomatal aperture is the loss of H_2O by transpiration (Monson and Grant 1989). The relationship between photosynthesis and transpiration is often expressed in terms of water-use efficiency, which is the quotient of carbon assimilation and transpiration (Sinclair et al. 1984). Water-use efficiency is one physiological component that may be important to the ability of plants to survive and grow under drought conditions (Aitken et al. 1995). Wittwer (1975) identified water as the second-most limiting factor, after land area, for increasing food production. Physiological processes of forest trees are inhibited more often by water stress than any other single factor (Kramer 1986). Growth is reduced directly by decreased cell enlargement and indirectly because of decreased leaf area, stomatal closure, and damage to the photosynthetic machinery. All of these effects reduce the photosynthetic production of the whole plant and decrease the amount of carbohydrate available for growth (Kramer 1986; Bongarten and Teskey 1987).

Forest trees respond to water limitation differently. For instance, Monson and Grant (1989) found that in adapting to drier habitats, ponderosa pine has acquired improved water-use efficiency and lower transpiration rate, but at the expense of reduced maximum photosynthetic rate. Osório and Pereira (1994) observed increased water-use efficiency in *Eucalyptus globulus* under water limitation as a consequence of changes in

stomatal conductance. Gibson et al. (1995) observed both morphological and physiological changes in *E. camaldulensis* seedlings grown from seeds collected from different habitats. Under water limitation, seedlings from the dry tropical and semi-arid climates had a higher allocation of dry matter to roots than seedlings from the humid tropics. In contrast, seedlings from the humid tropics responded to water limitation by reduced gas (CO_2 and H_2O) exchange without changes in morphology or allocation of dry matter.

Plant species which occupy either a large geographic range or a variety of contrasting habitats often exhibit genotypes that are adapted to local environmental conditions (Berry and Bjorkman 1980). Knowledge of genetic variation in physiological responses to varying environmental conditions is thus essential for the identification and selection of plant species or genotypes that are suitable to sites where water may at times be limiting.

Genetic resources are the foundation of biological diversity, which forms the essential link between evolution in the past and future adaptation to environmental change (Yeatman 1987). Forests contain a wealth of genetic resources of present-day use to human beings, and thus forest lands should be sustainably managed to meet social, economic, ecological, cultural, and spiritual human needs of present and future generations (McNeely 1994). However, sustainable management of genetic resources, as well as preserving the genetic diversity of a species, requires knowledge regarding the pattern and distribution of genetic diversity within and among populations (Hamrick et al. 1991; Yang and Yeh 1992). As previously reviewed, genetic variation can be assessed by various approaches. Ideally, genetic information used in conservation should incorporate

both adaptive and biochemical genetic data (Boyle et al. 1994). This is because one does not know *a priori* the relationship between the pattern of biochemical genetic variation and variation for adaptive quantitative traits in a given species. Consequently, the goals of the research reported in this thesis were to investigate pattern and distribution of genetic variation in *P. macrocarpus* by means of isozyme analysis (biochemical approach) and by evaluation of quantitative traits (growth, morphological and physiological traits), and to investigate physiological responses to water stress of this species.

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CHAPTER 2

ISOZYME VARIATION IN *PTEROCARPUS MACROCARPUS* [1]

2.1 Introduction

Current accumulation of knowledge from isozyme studies on the genetic structure of tropical woody species shows that they possess high levels of genetic variation and among-population differentiation (Hamrick et al. 1992; Loveless 1992; Moran 1992). Life history and ecological characteristics have been cited as factors influencing the amount and distribution of genetic variation (Hamrick et al. 1981; 1992). In developing countries that are largely in the tropics, habitat loss and fragmentation, over exploitation and the introduction of exotic species are decisive factors in the rapid destruction of tropical forests (Soulé 1991), which have been estimated to be home to at least two-thirds of the world's organisms (Raven 1986). Therefore, the persistence of evolutionary viable populations of tropical forests is crucial to the preservation of the tropical ecosystems and global biological diversity.

In tropical Asia, the United Nations (1986) estimated the loss of closed forest amounts to an annual rate of 1.8 million hectares (5,000 hectares per day) during the period 1976-1985. An annual loss of 3.2% of closed forest was estimated to have occurred in Thailand. A major cause of this deforestation is population pressure, and the resultant demands for fuelwood and extension of grazing areas and agricultural land.

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[1] *A version of this chapter has been published. Liengsiri, C., F.C. Yeh, and T.J.B. Boyle 1995. Forest Ecology and Management. 74:13-22.*

Integrated management of tropical ecosystems has the potential maintain stable, productive and sustainable forest resources. However, development of such an integrated management strategy would require that many aspects of the species' biology, ecology and genetics be thoroughly understood (Soulé 1991; Loveless 1992).

Pterocarpus macrocarpus Kurz is an important leguminous tree of southeast Asia. Its natural distribution extends from Burma through Thailand, Laos and Cambodia to southern Vietnam (Troup 1921; Rojo 1977). It is a commercially valuable timber not only in Thailand but also in the international timber trade (Anonymous 1979). In 1988, *P. macrocarpus* was the second most valuable export tree in Thailand, after teak *(Tectona grandis* L.), earning over 11 million dollars in US currency (Royal Forest Department 1989). Despite its economic and ecological importance there has been little effort to investigate its biological, ecological and genetic structure, and to develop the management strategy that is required for maintaining a stable, productive and sustainable forest resource. Currently, timber is harvested from natural *P. macrocarpus* forests and in the long-run, will lead to an accelerated loss of its genetic resources. This will result in reduced potential and opportunity for breeding, genetic improvement and resource management, and conservation. The objective of this study was to investigate the amount and distribution of genetic variation in natural populations of *P. macrocarpus* sampled from different forest habitats in Thailand by means of isozyme analysis.

2.2 Materials and methods

Seeds of *P. macrocarpus* were collected from 11 natural populations representing different forest habitats in Thailand (Figure 2.1). Details of population locations, climatic

information, and number of sampled trees are given in Table 2.1. Mixed deciduous and hill evergreen forests represent a deep soil and moist habitat, whereas dry dipterocarp forest represents a shallow soil and dry habitat. From each sampled tree, indehiscent samaras (flat round-winged pods) were collected throughout its crown with a minimum of 1,000 pods being collected. Seeds were extracted manually and kept separate by mother tree.

Horizontal starch gel electrophoresis for isozymes surveyed followed the procedures described by Liengsiri et al. (1990a; 1990b). Twenty emerging radicles of germinating seeds (3-4 days under ambient condition, 25-30°C) from each sampled tree were individually assayed for variation at 11 enzyme systems (Table 2.2). For enzyme systems with multiple loci, the most anodal migrating locus (fastest locus) was assigned as 1 and other loci were assigned increasing numbers with decreasing migrating distance. At each locus, the most common allele was arbitrarily designated as 1 and the others as 2, 3, and so on.

Data analysis was performed on the progeny arrays of sampled trees using BIOSYS-1 (Swofford and Selander 1989). Four measures of genetic diversity were computed. They were percentage of polymorphic loci (P) at the 0.99 criterion, average number of alleles per locus (A), observed (H_O) and expected heterozygosity (H_E).

The partitioning of total variation into within- and among-population variation followed Wright's F-statistics (Wright 1965). Nei's (1972) pair-wise genetic distances (D) were calculated and the estimate used in a hierarchical cluster analysis of populations using UPGMA (Sneath and Sokal 1973). The Pearson correlation between genetic and geographic distances among populations was computed to determine their relationship.

Linear correlations were also computed to detect possible relationships between geographic variables of populations (latitude, longitude and elevation) and their common allele frequencies.

2.3 Results

Allele frequencies of the populations are given in Table 2.3. All 18 loci were polymorphic at the 0.99 criterion in at least one population. Allele 1 was common in most populations and homogeneity tests suggest its frequency varied significantly among the populations, except for the loci *AAT-1*, *AAT-2*, *AAT-3*, *EST*, *PGI-2* and *ME-2*. The least variable locus was *MR-2*, at which populations were mostly monomorphic and the frequency of the common allele at the two variable populations (5 and 11) was over 0.97. Locus *6PG-2* was the most variable with seven alleles, although they were not all present in any one population. Only *AAT-3* showed an east-west trend of different alleles, with eastern populations (6 to 11, except 8) dominated by allele 2 with allele 1 being common in western populations (1 to 5). Null alleles were observed at three loci (*MDH-2*, *MR-3* and *6PG-2*).

Several populations had unique alleles at some loci (Table 2.3). They included population 3 (allele 4 at *6PG-3*), population 5 (allele 3 at *ADH* and null allele at *MHD-2*), population 7 (allele 6 at *6PG-2*) and population 8 (allele 4 at *AAT-1*). Khong-chiam (population 11) was the most divergent of the populations, exhibiting large frequency differences in its common alleles from the other populations at many loci (Table 2.3). Its most striking locus was *6PG-2*, at which the null allele was the common allele (Table 2.3).

The measures of genetic diversity suggest a high level of genetic variability within populations (Table 2.4). On average, single populations were polymorphic at 82.32% of their loci and the range was from 66.67 to 100% among the populations. The loci segregated for two to seven alleles, but the norm was three to four alleles at most loci (Table 2.3). The number of alleles per locus per population ranged between 2.44 to 2.94, averaging 2.67 for the sampled populations. Observed heterozygosity per population (H_O) varied between 0.185 to 0.246 and with an average of 0.222. The average of observed heterozygosity (0.222) is 11% lower than the average of expected heterozygosity (0.246). Except for population 1 that had a slight excess of heterozygotes, all other populations exhibited heterozygote deficiencies.

F-statistics revealed varying fixation indices among the loci (Table 2.5). The estimates of F_{IS} revealed two loci (*MDH-1* and *MR*-2) with an excess of heterozygotes. The 16 remaining loci each exhibited heterozygote deficiency. Genetic differentiation among populations as measured by F_{ST} showed that 12.1% of the total genetic variation was due to differences among populations; 87.9% of the isozyme variation resided within populations (Table 2.5). The loci with sizable among-population differentiation were *AAT-1*, *AAT*-3, *EST*, *PGI-2* and *ME*-2.

Nei's genetic distances (*D*) between populations (Table 2.6) averaged 0.051 (SD = 0.026) and ranged from 0.012 to 0.110. Generally, population pairs with smaller geographic separation (Figure 2.1; Table 2.6) were genetically more similar (low *D*) than population pairs with greater geographic isolation. This evidence was supported by a very significant correlation between genetic and geographic distances ($r = 0.515$; $P < 0.0001$), implying that geographic variation contributed approximately 26.5% to the genetic

differentiation among populations. The UPGMA cluster analysis using Nei's genetic distance coefficients provides a clearer picture of population grouping (Figure 2.2) that reflects the size of geographic isolation along longitudinal gradient (east-west direction). Khong-chiam (population 11), the easternmost population, was separated completely from the other populations (Figure 2.2). Population 5 despite being geographically proximate to population 4, grouped with population 2 that aligned on similar longitude (Figure 2.1; Table 2.1). This longitudinal trend of population grouping was apparent from the correlation analysis between longitudes of populations and their frequencies at eight loci (Table 2.7).

2.4 Discussion

P. macrocarpus from Thailand possesses a high level of genetic diversity. The percentage of polymorphic loci averaged 82.32% among 11 populations. This is higher than the reported 67.7% for conifers (Hamrick et al. 1981), 60.9% for tropical trees from central America (Hamrick and Loveless 1989) and 56.3% for trees from Australia (Moran 1992). However, *Acacia albida* from Africa was more polymorphic (90%), although detected at the 95% criterion (Joly et al. 1992). Parallel to the percentage of polymorphic loci, average number of alleles per locus in *P. macrocarpus* (2.67) was greater than that found in conifers (2.29) (Hamrick et al. 1981), tropical trees from central America (2.02) (Loveless and Hamrick 1987) and Australian trees (1.88) (Moran 1992), but is much lower than that reported for African acacia (4.3) (Joly et al. 1992).

The observed (0.222) and expected (0.246) heterozygosities are comparable to the reported 0.211 and 0.207 averages for other tropical trees (Hamrick and Loveless 1989)

and conifers (Hamrick et al. 1981), respectively. Heterozygosity estimates in *P. macrocarpus* are higher than the 0.17 estimate in Australian species (Moran 1992) but lower than the observed (0.304) and expected (0.454) estimates in African acacia (Joly et al. 1992). With the observation that ten of the populations had homozygote excess and that the estimate of F_{IS} was positive at 0.099, our results suggest that inbreeding and selfing could have occurred in most populations (Tables 2.4 and 2.5).

P. macrocarpus has a perfect flower and the pollination mechanism relies mainly on insects as pollinators. The movement of pollinators among adjacent flowers within the crown or between adjacent crowns of related neighbours might be confined to a short distance and this would increase inbreeding and selfing within populations (Levin and Kerster 1968). Although recent finding has revealed that most tropical trees appear to experience a great deal of long-distance pollen movement (e.g. Nason et al. 1996; Nason and Hamrick 1997), pollen dispersal of *P. macrocarpus* has not yet been investigated. In addition, the limitation of wind dispersal of samaras (round-winged pods) could create family structure that elevate the frequency of inbreeding events in this species. However, there is no documented study on the amount of seed dispersal in *P. macrocarpus*. Hamrick and Loveless (1989) suggested that mode of pollen and seed dispersal could have a major influence on the degree of within-population genetic diversity as reflected in observed and expected heterozygosities.

The level of population differentiation in *P. macrocarpus* as measured by F_{ST} (12.1%) is similar to that reported for other tropical trees (Butcher et al. 1992; Hamrick et al. 1992; Joly et al. 1992; Soonhuae 1993). This level of population subdivision is somewhat higher when compared to that of temperate tree species and supports the notion

that there is greater population differentiation in the tropics than in the temperate zone (Hamrick et al. 1992). Possible reasons for higher levels of population differentiation in tropical species have been reviewed by Bawa (1976). They include lower population densities, more widely scattered populations that reduce gene flow and increase genetic drift, and greater spatial variation in natural selection pressure. In addition, the mode of pollen and seed dispersal also influences genetic differentiation since wind-pollinated species exhibit less among-population genetic differentiation than animal-pollinated species (Loveless and Hamrick 1987). Yeh (1989) listed values of G_{ST} for some wind-pollinated temperate species that ranged from 0.01 for *Picea mariana* to 0.079 for *Picea sitchensis*. Boyle et al. (1991) also reported low G_{ST} (0.039) for *Pinus kesiya*, a wind-pollinated tropical pine. These G_{ST} estimates for wind-pollinated trees are much lower than the 0.121 in *P. macrocarpus* (Table 2.5) and that of other species whose breeding system relies on animals as pollinators (averaged $G_{ST} = 0.122$, Hamrick et al. 1992).

Species that are widespread exhibit high levels of among-population genetic differentiation (Joly et al. 1992; Moran 1992), especially in association with a disjunct distribution (Moran et al. 1989b; Xie et al. 1992) and small population size (Xie et al. 1992). This conclusion is evident in *P. macrocarpus*, a tree with a wide range and disjunct distribution that extends from Burma to southern Vietnam (Rojo 1977). Genetic and geographic distances (Table 2.6) revealed strong correlations ($r = 0.515$; $P < 0.0001$), which suggests that isolation by distance could be a significant cause of population differentiation in *P. macrocarpus*. Correlations between genetic and geographic distances have also been reported in *Psuedotsuga menziesii* (Yeh and O'Malley 1980), *Melaleuca alternifolia* (Butcher et al. 1992), *Ulmus crassifolia* (Sherman-Broyles et al. 1992),

Populus tremuloides (Chong et al. 1994) and some Australian species (Moran 1992). The grouping of populations by cluster analysis followed an east-west population distribution (Figures 2.1 and 2.2), probably the result of significant correlation between longitude and allele frequencies at eight loci (Table 2.7). This was similar to the report in *Casuarina cunninghamiana* that grouping of populations followed a latitudinal distribution (Moran et al. 1989a). Since all my populations were sampled in Thailand, it would be of interest to investigate if the longitudinal grouping of the populations would persist throughout the natural range of *P. macrocarpus* in southeast Asia. If so, would it be possible to delineate zoning of this species for breeding and deployment along its longitudinal natural distribution range?

Long-lived woody perennials in association with other life history and ecological characteristics generally possess high level of genetic diversity (Hamrick et al. 1992). This conclusion is well supported by this and other studies reviewed previously. High genetic differentiation among populations of widespread tropical species due to geographic isolation was supported by this study and others discussed previously. The prominent longitudinal differentiation of the populations suggests that an optimal strategy for *ex situ* conservation of *P. macrocarpus* in Thailand would be to sample seeds from a few trees in each of many populations to include a wide spectrum of the east-west environment. Although the fine-scale genetic structure of *P. macrocarpus* has not yet been investigated, distance between trees within populations should be maintained at least 100 meters to reduce the risk of sampling relatives. Populations that exhibit significant genetic differentiation such as Khong-chiam (population 11) would be the obvious targets for sampling. Such a scheme is analogous to the sampling of locally common genes in

forest populations (Yang and Yeh 1992). Further analysis of the pattern of genetic diversity across the whole natural range is a prerequisite to effective development and implementation of breeding and genetic resources conservation strategies (Brown 1978; Yeh 1989), especially for *P. macrocarpus* that is under threat from rapid deforestation and genetic erosion. Thus, germplasm collections in *P. macrocarpus* should not be restricted by political boundaries but should be aimed at the whole species range (Boyle et al. 1994) to assure adequate sampling of the genome for conservation.

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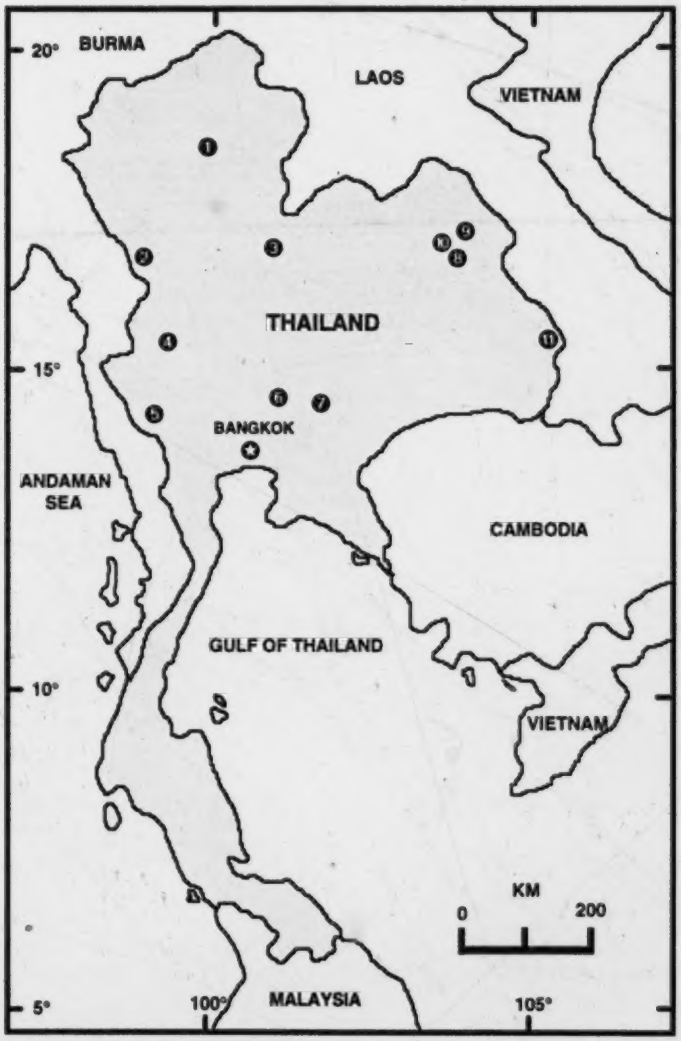

Figure 2.1 Map of Thailand showing locations of 11 sampled populations of *P. macrocarpus*.

Table 2.1 Geographic location, elevation, climate, forest type and number of sampled trees of 11 populations of *P. macrocarpus*.

Population		Latitude (°N)	Longitude (°E)	Elevation (m)	Mean annual temperature (°C)	Annual rainfall (mm)	Forest type [a]	No. of sampled trees
No.	Name							
1	Lampang	18°35'	99°54'	350	25.9 [b]	1076 [b]	MDF	15
2	Tak	16°42'	98°57'	600	27.3 [b]	1063 [b]	MDF	15
3	Pitsanulok	16°50'	100°53'	500	27.5 [b]	1351 [b]	MDF	15
4	Uthaithani	15°30'	99°22'	220	N/A	N/A	DDF	34
5	Kanchanaburi	14°15'	99°10'	500	27.9 [b]	1051 [b]	MDF	17
6	Saraburi	14°35'	101°12'	200	26.1 [c]	1168 [c]	MDF	33
7	Sakaerat	14°25'	101°45'	380	26.3 [d]	1310 [d]	DDF	106
8	Phuphan-1	16°48'	103°53'	480	26.1 [b]	1587 [b]	HGF	15
9	Phuphan-2	17°02'	103°57'	240	26.1 [b]	1587 [b]	DDF	7
10	Phuphan-3	16°58'	103°45'	310	26.1 [b]	1587 [b]	DDF	15
11	Khong-chiam	15°24'	105°29'	200	26.7 [b]	1634 [b]	DDF	15

[a] MDF: mixed deciduous forest (moist site); DDF: dry dipterocarp forest (dry site); HGF: hill evergreen forest (moist site).
[b] Meteorological Department, Bangkok, Thailand (1961-1990).
[c] Thai-Danish Dairy Farm, Saraburi, Thailand (1976-1990).
[d] Sakaerat Environmental Research Station, Nakhonratchasima, Thailand (1980-1989).
N/A: data not available.

Table 2.2 Enzyme systems assayed in *P. macrocarpus.*[a]

Enzyme system	Abbreviation	EC code	No. of loci
Aspartate aminotransferase	*AAT*	2.6.1.1	3
Alcohol dehydrogenase	*ADH*	1.1.1.1	1
Acid phosphatase	*APH*	3.1.3.2	1
Esterase	*EST*	3.1.1.1	1
Isocitrate dehydrogenase	*IDH*	1.1.1.42	1
Phosphoglucose isomerase	*PGI*	5.3.1.9	1
Phosphoglucomutase	*PGM*	2.7.5.1	2
Malate dehydrogenase	*MDH*	1.1.1.37	2
Malic enzyme	*ME*	1.1.1.40	1
Menadione reductase	*MR*	1.6.99.2	2
6-Phosphogluconic dehydrogenase	*6PG*	1.1.1.44	3

[a] Extraction buffer No. 10 and H buffer system as described by Liengsiri et al. (1990a) were used. Initial current was 40 mA for approximately 40 minutes and re-run current after dewicking was 80 mA until dye-front migrating to 7 cm. 12.5% starch gel was used.

Table 2.3 Allele frequencies of 18 loci in 11 populations of *P. macrocarpus*.

Locus	Allele	Population 1	2	3	4	5	6	7	8	9	10	11
AAT-1	1	0.923	0.627	0.958	0.928	0.840	0.261	0.531	0.627	0.704	0.602	0.763
	2	0.077	0.353	0.042	0.072	0.160	0.739	0.435	0.343	0.296	0.393	0.195
	3		0.020					0.034	0.008		0.005	0.042
	4								0.022			
AAT-2	1	0.360	0.547	0.337	0.800	0.582	0.478	0.671	0.425	0.318	0.435	0.443
	2	0.513	0.450	0.602	0.081	0.291	0.233	0.233	0.573	0.675	0.565	0.512
	3	0.127	0.003	0.062	0.112	0.074	0.288	0.095	0.002	0.007		0.005
	4				0.007	0.053	0.001	0.001				0.040
AAT-3	1	0.677	0.663	0.768	0.710	0.815	0.182	0.187	0.587	0.375	0.375	0.015
	2	0.323	0.337	0.220	0.290	0.185	0.817	0.780	0.393	0.625	0.625	0.962
	3			0.012			0.001	0.033	0.020			0.023
ADH	1	1.000	0.968	1.000	0.944	0.963	0.986	0.997	1.000	1.000	1.000	1.000
	2		0.032		0.056		0.014	0.003				
	3					0.037						
APH-2	1	0.847	0.890	0.728	0.671	0.797	0.996	0.914	0.782	0.729	0.712	0.585
	2	0.132	0.108	0.248	0.324	0.203	0.003	0.059	0.218	0.264	0.267	0.415
	3	0.022	0.002	0.007	0.005					0.004	0.005	
	4			0.017	0.001		0.001	0.027		0.004	0.017	
EST	1	0.945	0.828	0.643	0.602	0.776	0.433	0.492	0.393	0.718	0.607	0.912
	2	0.002	0.075	0.028					0.125	0.125	0.003	0.003
	3	0.053	0.097	0.327	0.398	0.224	0.529	0.502	0.480	0.157	0.390	0.085
	4			0.002			0.038	0.006	0.002			

Table 2.3 Continued.

Locus	Allele	Population 1	2	3	4	5	6	7	8	9	10	11
IDH	1	0.967	0.873	0.857	0.761	0.759	0.928	0.994	0.937	0.989	0.848	0.878
	2	0.007	0.113	0.080	0.207	0.232	0.072	0.004	0.063	0.007	0.148	
	3	0.012	0.013	0.027	0.001	0.009				0.004	0.003	0.122
	4	0.015		0.037								
	5				0.032			0.002				
PGI-2	1	1.000	0.963	0.932	0.823	0.979	0.927	0.776	0.935	0.846	0.782	0.442
	2		0.037	0.068	0.160		0.071	0.194	0.062	0.061	0.217	0.558
	3				0.004	0.001		0.002	0.003	0.079	0.002	
	4				0.013	0.019	0.002	0.028		0.014		
PGM-1	1	0.983	0.985	0.997	0.989	0.985	1.000	1.000	1.000	1.000	0.997	0.965
	2	0.017	0.012	0.003	0.011	0.015					0.003	0.008
	3		0.003									0.027
PGM-2	1	0.952	0.998	1.000	0.975	0.979	0.972	0.947	0.962	1.000	0.997	0.725
	2	0.048	0.002		0.001		0.017					0.212
	3				0.024	0.021	0.011	0.053	0.038		0.003	0.063
MDH-1	1	0.818	0.873	0.958	0.942	0.781	0.974	0.969	0.987	0.957	1.000	0.965
	2	0.182	0.058	0.003	0.057	0.219	0.010	0.030	0.010	0.043		0.035
	3		0.068	0.038	0.001		0.016	0.002	0.003			
MDH-2	1	0.983	0.947	0.982	0.978	0.951	1.000	0.999	1.000	1.000	1.000	0.985
	2	0.013	0.053	0.018	0.021	0.034		0.001				0.015
	3	0.003			0.001							
	Null					0.015						

Table 2.3 Continued.

Locus	Allele	Population										
		1	2	3	4	5	6	7	8	9	10	11
ME-2	1	0.888	0.913	0.770	0.938	0.938	0.880	0.898	0.393	0.511	0.523	0.917
	2	0.107	0.063	0.127	0.061	0.053	0.117	0.047	0.067	0.321	0.102	0.002
	3	0.005	0.023	0.103	0.001	0.009	0.003	0.055	0.540	0.168	0.375	0.082
MR-2	1	1.000	1.000	1.000	0.993	0.979	0.998	1.000	1.000	1.000	1.000	0.983
	2				0.007	0.021	0.002					0.017
MR-3	1	0.862	0.810	0.597	0.647	0.765	0.612	0.719	0.685	0.436	0.607	0.605
	2	0.138	0.190	0.403	0.353	0.194	0.388	0.281	0.315	0.336	0.333	0.353
	3					0.041				0.100	0.060	0.002
	Null									0.129		0.040
6PG-1	1	0.723	0.867	0.707	0.654	0.800	0.900	0.883	0.958	0.800	0.985	0.917
	2	0.275	0.125	0.247	0.346	0.200	0.099	0.117	0.037	0.196	0.015	0.082
	3	0.002	0.003	0.047						0.004		0.002
	4		0.005				0.001		0.005			
6PG-2	1	0.525	0.612	0.690	0.712	0.629	0.721	0.551	0.665	0.632	0.695	0.295
	2	0.300	0.252	0.155	0.184	0.160	0.152	0.092	0.108	0.046	0.118	0.027
	3	0.117	0.042	0.090	0.054	0.028	0.033	0.070	0.085	0.068	0.117	0.070
	4	0.013	0.052	0.055	0.007	0.076	0.015	0.175	0.080	0.254	0.062	0.013
	5	0.045	0.043	0.010	0.043	0.106	0.073	0.095	0.062		0.008	0.202
	6							0.016				
	Null						0.006					0.393
6PG-3	1	0.845	0.813	0.863	0.724	0.712	0.856	0.885	0.867	0.975	0.745	0.897
	2	0.152	0.178	0.092	0.275	0.287	0.136	0.115	0.113	0.025	0.253	0.103
	3	0.003	0.008	0.028	0.001	0.001	0.008		0.020		0.002	
	4			0.017								

Table 2.4 Measures of genetic variability in 11 populations of *P. macrocarpus*: percentage of loci polymorphic (P, at 99% criterion), mean number of alleles per locus (A), observed heterozygosity (H_O) and expected heterozygosity (H_E) averaged over all loci (standard errors in parentheses).

Population					
No.	Name	P	A	H_O	H_E
1	Lampang	83.33	2.50 (0.25)	0.212 (0.046)	0.210 (0.046)
2	Tak	88.89	2.72 (0.21)	0.233 (0.041)	0.234 (0.041)
3	Pitsanulok	77.78	2.72 (0.28)	0.235 (0.046)	0.244 (0.047)
4	Uthaithani	94.44	2.89 (0.23)	0.239 (0.039)	0.262 (0.042)
5	Kanchanaburi	100.00	2.61 (0.20)	0.246 (0.042)	0.257 (0.042)
6	Saraburi	77.78	2.72 (0.27)	0.191 (0.044)	0.213 (0.048)
7	Sakaerat	72.22	2.94 (0.26)	0.225 (0.049)	0.235 (0.050)
8	Phuphan-1	77.78	2.56 (0.27)	0.231 (0.049)	0.255 (0.054)
9	Phuphan-2	72.22	2.44 (0.27)	0.185 (0.040)	0.263 (0.057)
10	Phuphan-3	66.67	2.44 (0.26)	0.235 (0.047)	0.275 (0.054)
11	Khong-chiam	94.44	2.78 (0.26)	0.206 (0.038)	0.260 (0.051)
	Average	82.32 (3.25)	2.67 (0.05)	0.222 (0.010)	0.246 (0.011)

Table 2.5 Summary of *F*-statistics at 18 loci in *P. macrocarpus*.

Locus	F_{IS}	F_{IT}	F_{ST}
AAT-1	0.090	0.258	0.185
AAT-2	0.084	0.180	0.105
AAT-3	0.100	0.335	0.261
ADH	0.037	0.066	0.030
APH-2	0.131	0.197	0.077
EST	0.241	0.343	0.135
IDH	0.040	0.105	0.068
PGI-2	0.060	0.233	0.184
PGM-1	0.015	0.027	0.011
PGM-2	0.013	0.124	0.113
MDH-1	-0.150	-0.062	0.076
MDH-2	0.121	0.139	0.020
ME-2	0.295	0.432	0.195
MR-2	-0.017	-0.004	0.012
MR-3	0.041	0.087	0.048
6PG-1	0.088	0.156	0.074
6PG-2	0.082	0.147	0.071
6PG-3	0.029	0.071	0.044
Mean	0.099	0.208	0.121

Table 2.6 Nei's genetic distances (above diagonal) and geographic distances (below diagonal) between 11 populations of *P. macrocarpus*.

Population		1	2	3	4	5	6	7	8	9	10	11
1	Lampang	***	0.013	0.019	0.039	0.016	0.086	0.060	0.058	0.042	0.055	0.089
2	Tak	200.0	***	0.024	0.033	0.012	0.051	0.037	0.040	0.037	0.034	0.085
3	Pitsanulok	212.5	212.5	***	0.026	0.021	0.083	0.060	0.032	0.030	0.037	0.097
4	Uthaithani	325.0	150.0	220.8	***	0.016	0.079	0.051	0.062	0.068	0.055	0.103
5	Kanchanaburi	445.8	262.5	325.0	120.8	***	0.080	0.057	0.053	0.058	0.051	0.110
6	Saraburi	420.8	320.8	225.0	200.0	208.3	***	0.014	0.056	0.058	0.040	0.096
7	Sakaerat	466.7	387.5	258.3	270.8	275.0	75.0	***	0.044	0.043	0.029	0.059
8	Phuphan-1	445.8	508.3	291.7	487.5	554.2	362.5	325.0	***	0.030	0.013	0.105
9	Phuphan-2	437.5	512.5	304.2	504.2	575.0	391.7	358.3	37.5	***	0.022	0.066
10	Phuphan-3	416.7	487.5	279.2	475.0	545.8	362.5	333.3	29.2	27.5	***	0.063
11	Khong-chiam	645.8	683.3	475.0	629.2	666.7	462.5	395.8	208.3	225.0	237.5	***

Table 2.7 Coefficient of correlation between geographic variables and frequency of common allele in 11 populations of *P. macrocarpus*.

Locus	Latitude	Longitude	Elevation
AAT-1	0.380 ns	-0.255 ns	0.192 ns
AAT-2	0.706 *	0.543 ns	0.197 ns
AAT-3	0.325 ns	-0.696 *	0.633 *
ADH	0.404 ns	0.695 *	-0.092 ns
APH-2	-0.182 ns	-0.463 ns	-0.269 ns
EST	0.350 ns	-0.145 ns	0.059 ns
IDH	0.305 ns	0.401 ns	-0.138 ns
PGI-2	0.264 ns	-0.684 *	0.558 ns
PGM-1	0.017 ns	-0.018 ns	0.098 ns
PGM-2	0.211 ns	-0.521 ns	0.400 ns
MDH-1	-0.055 ns	0.681 *	-0.420 ns
MDH-2	0.107 ns	0.687 *	-0.591 ns
ME-2	-0.448 ns	-0.611 *	-0.026 ns
MR-2	0.556 ns	0.024 ns	0.108 ns
MR-3	0.083 ns	-0.627 *	0.548 ns
6PG-1	-0.158 ns	0.616 *	0.001 ns
6PG-2	0.022 ns	-0.398 ns	0.185 ns
6PG-3	0.221 ns	0.555 ns	-0.211 ns

ns: non-significant at $P < 0.05$; *: significant at $P < 0.05$.

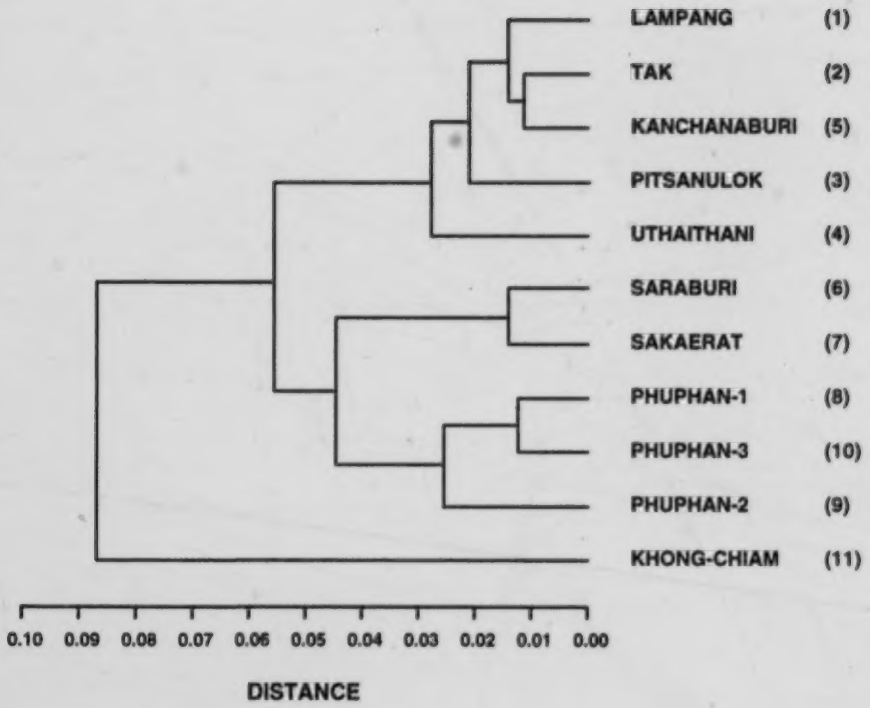

Figure 2.2 Cluster analysis of 11 populations of *P. macrocarpus* using Nei's (1972) genetic distance coefficients and UPGMA.

CHAPTER 3

MATING SYSTEM IN *PTEROCARPUS MACROCARPUS* [1]

3.1 Introduction

The mating system is an important determinant of the genetic structure and evolutionary potential of natural populations because it establishes the pattern of uniting gametes to form the next generation (Allard 1975). Plants exhibit a wide variety of mating structures including: (1) regular systems of inbreeding and frequently self-fertilization, (2) negative assortative mating due to various kinds of incompatibility systems, and (3) effective inbreeding due to the clustering of related individuals within a small neighborhood (Clegg 1980). Brown (1990) further classified plant mating systems into five major modes: (1) predominant selfing (with outcrossing rate, $t < 0.1$), (2) predominant outcrossing (self-fertilization rate, $s < 0.05$), (3) mixed selfing and outcrossing, (4) facultative or obligate apomixis, and (5) intragametophytic or haploid selfing. Hamrick et al. (1979) demonstrated that plant species characterized by high levels of outcrossing typically maintain high genetic diversity, with relatively small differences among populations and high within-population variation.

Although morphological markers could estimate the outcrossing rate in plant populations (e.g., Morgenstern 1972), isozyme markers have greatly facilitated the study of mating systems because of several distinct advantages over morphological markers. These are: (1) allozymes are codominantly expressed, (2) many isozyme loci are highly

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[1] *A version of this chapter has been published. Liengsiri, C., T.J.B. Boyle, and F.C. Yeh 1998. Journal of Heredity. 89:216-221.*

polymorphic in most populations, and (3) allozymes are unlikely themselves to be subject to strong selective forces (Brown et al. 1989). As a consequence, quantitative estimates of outcrossing rates in plant populations have accumulated for the past decade (e.g., Brown et al. 1975; Moran and Brown 1980; Yeh and Morgan 1987). In tropical forests, tree species typically occur at low density, and the resultant partial isolation led to speculation that most tropical species are self-pollinated and inbred (Fedorov 1966). However, recent work has shown that most tropical tree species are self-incompatible or dioecious (Bawa et al. 1985). This has been supported by high quantitative estimates of outcrossing rates (>80% to 100%) in many species (Nason and Hamrick 1997). However, some species display low outcrossing rates and a mixed mating system, for example, *Cavanillesia platanifolia* (ranging from 0.213 to 0.569) and *Ceiba pentandra* (0.689).

The mating system is dynamic and can vary in space and time. For instance, Godt and Hamrick (1991) reported significant heterogeneity in outcrossing rates among seven populations in *Lathyrus latifolius* and Murawski et al. (1994) reported tree-to-tree variation and year-to-year variation in outcrossing rates in *Shorea trapezifolia*. A number of ecological factors affect this variation, including the mode of pollination, the architectural complexity of individuals flowers and plants, and the size and density of populations (Brown et al. 1989). Among these factors, the mode of pollination seems to have a major impact on the pattern of outcrossing. Schemske and Lande (1985) reported a bimodal distribution of outcrossing rates observed in natural plant populations with primarily selfing and primarily outcrossing, but Aide (1986) noted that a bimodal distribution was found only in wind-pollinated species and can not be detected for animal-pollinated species.

Pterocarpus macrocarpus Kurz is an important timber species of southeast Asia with a natural distribution extending from Burma through Thailand, Laos and Cambodia to southern Vietnam (Rojo 1977). Trees are generally found scattered in mixed deciduous forest, dry dipterocarp forest and hill evergreen forest with altitudes ranging from 100 to 600 meters. It has a perfect flower which relies on insects as pollinators. Although individual flowers have a short blooming period lasting only a few hours in the morning, individual trees generally produce abundant flowers and the flowering episode within each tree lasts for 2 to 3 weeks (Liengsiri 1997). Isozyme analysis has revealed high levels of genetic diversity and a high degree of among-population differentiation with an east-west pattern of population grouping (Chapter 2). Estimates of outcrossing rates in plant populations have been reported for several tropical species (e.g., O'Malley and Bawa 1987; Murawski and Hamrick 1991; Murawski and Bawa 1994; Murawski et al. 1994; Kjær and Suangtho 1995). However, little is known about the characteristics of among-population outcrossing rates and to what extent the within-population variation in outcrossing rates affects population estimates, particularly across the species range. This study investigated the mating system of 11 natural populations sampled across forest types (habitat characteristics, degree of disturbance, and density) in Thailand using isozyme markers at 16 loci.

3.2 Materials and methods

Seeds of *P. macrocarpus* were collected from 11 natural populations representing different forest habitats in Thailand (Figure 3.1; Table 3.1). Populations 1, 2, 3, 5 and 6 were sampled from mixed deciduous forest and population 8 was sampled from hill

evergreen forest. These six populations are from moist habitats. Populations 4, 7, 9, 10 and 11 were sampled from dry dipterocarp forest, the other habitat extreme. Generally, there was a greater degree of disturbance and lower density in eastern populations (populations 8, 9, 10 and 11) than in western populations (populations 1, 2, 3, 4, and 5) where the areas are protected. In eastern populations, habitats are much drier with poor and shallow soils as a consequence of deforestation and soil erosion. Trees in these populations were remnant and scattered and population density was less than 1.5 flowering individuals per hectare (Table 3.1). There is also occasional disturbance in these populations from nearby local inhabitants for fuel wood harvesting and cattle grazing from which it would further reduce population size and minimize regeneration potential. Western populations, on the other hand, are well protected in national parks and wildlife sanctuaries and population density was more than 2.5 flowering individuals per hectare (Table 3.1). There was also a high degree of disturbance in population 6 similar to eastern populations. Among 11 populations studied, population 7 was the largest population with high density and less disturbance. Details of population locations, density, and number of sampled trees are presented in Table 3.1. A minimum of 1,000 samaras (flat round-winged pods) were collected from each sampled tree. Seeds were extracted manually and kept separate by mother trees.

Twenty emerging radicles of germinating seeds (3-4 days under ambient conditions, 25-30°C) from each sampled tree were assayed for genotypes at 18 loci encoded by 11 enzyme systems using horizontal starch gel electrophoresis described by Liengsiri et al. (1990) and in Chapter 2. The 11 enzyme systems were aspartate aminotransferase (*AAT*; EC 2.6.1.1), alcohol dehydrogenase (*ADH*; EC 1.1.1.1), acid

phosphatase (*APH*; EC 3.1.3.2), esterase (*EST*; EC 3.1.1.1), isocitrate dehydrogenase (*IDH*; EC 1.1.1.42), phosphoglucose isomerase (*PGI*; EC 5.3.1.9), phosphoglucomutase (*PGM*; EC 2.7.5.1), malate dehydrogenase (*MDH*; EC 1.1.1.37), malic enzyme (*ME*; EC 1.1.1.40), menadione reductase (*MR*; EC 1.6.99.2), and 6-phosphogluconic dehydrogenase (*6PG*; EC 1.1.1.44). Only 16 loci that were polymorphic at 95% in at least one population were included in the analysis.

The multilocus mixed mating program (MLT) (Ritland 1990) was used to estimate single locus (t_s) and multilocus (t_m) outcrossing rates based on the mixed mating model of Ritland and Jain (1981). The model assumptions are (1) each mating event is a random outcross event (with probability t) or self-fertilization (with probability $s = 1 - t$), (2) the probability of an outcross is independent of maternal genotype, (3) outcross pollen allele frequencies are homogeneous among maternal genotypes, (4) selection does not occur between fertilization and the assay of progeny genotypes, and (5) alleles at different loci segregate independently (for multilocus estimates). The MLT program was also used to obtain maternal genotypes inferred from progeny arrays using the method of Brown and Allard (1970) and to estimate individual tree outcrossing rates (t_{mi}).

The observed inbreeding coefficient (F) of Wright (1965) was calculated for both progeny and parental populations as $F = 1 - (H_o/H_e)$, where H_o is the observed heterozygosity, $H_e = 1 - \sum p_i^2$ is the expected heterozygosity under random mating, and p_i is the frequency of the ith allele. The expected inbreeding coefficient at equilibrium (F_e) was calculated from multilocus outcrossing rate (t_m) by the equation of Fyfe and Bailey (1951) as $F_e = (1 - t_m)/(1 + t_m)$. This expected value ($F_e$) was compared to the observed values from progeny populations.

3.3 Results

Estimates of single-locus (t_s) and multilocus (t_m) outcrossing rates are presented in Table 3.2. Single-locus outcrossing rates varied within and among populations ranging from 0.021 for *ME-2* in population 9 to 0.999 for *MDH-1* in population 5. Eastern populations possessed lower t_s at more loci than did western populations. Average t_s and t_m also varied among populations ranging from 0.620 to 0.931 for t_s and from 0.719 to 0.959 for t_m. Although estimates of t_m were greater than the average t_s in all populations, the differences were not statistically significant. None of the average t_s was significantly less than 1 (that is $[t + 2SE] > 1$ for all populations), while the t_m of many populations was significantly less than 1 (Table 3.2). Both average t_s and t_m revealed a geographic pattern with western populations exhibiting higher outcrossing rates than eastern populations.

There were excess heterozygotes observed in all parental (adult) populations as indicated by the negative inbreeding coefficients (F_p) that ranged from −0.457 to −0.152 (Table 3.2). In contrast, progeny populations exhibited varying degrees of inbreeding and heterozygote deficit as indicated by the positive inbreeding coefficients (F_o) except populations 1 and 2 which were in random mating (Table 3.2). In all cases, the expected inbreeding coefficients at equilibrium (F_e) were positive and were lower than the observed inbreeding coefficients in progeny populations, except populations 1 and 2 (Table 3.2). This suggests that progeny populations contained fewer heterozygotes than expected.

Individual tree outcrossing rates (t_{mi}) were heterogeneous in each population (Figure 3.2). All populations exhibited predominant outcrossing with a large proportion

of trees having outcrossing rates equal to or greater than 0.90. The exception was populations 9 and 10 where 43% and 73%, respectively, of trees had outcrossing rates less than 0.90. These two populations also had low population average t_s and t_m (Table 3.2).

3.4 Discussion

The high estimates of outcrossing rates (Table 3.2) suggest that *P. macrocarpus* is predominantly an outcrossing species. The average t_s (0.819) and t_m (0.899) over 11 populations are comparable to those reported for other palaeotropical and neotropical species (Kjær and Suangtho 1995; Nason and Hamrick 1997).

Single-locus estimates of outcrossing rates (t_s) were variable in all populations (Table 3.2). Heterogeneous estimates of t_s among isozymes are common among forest trees and have been reported for conifers (e.g., Boyle et al. 1991; Xie et al. 1991), eucalypts (e.g., Brown et al. 1975; Moran and Brown 1980), and tropical species (e.g., O'Malley and Bawa 1987; Kjær and Suangtho 1995). Theoretically, the estimates of mating system parameters from a common set of embryos are expected to be homogeneous over loci because the mating process should have an identical effect on all loci (Clegg 1980). Thus, inter-locus heterogeneity of estimates may be due to variation in information among loci to detect outcrossing events and estimate the rate (Yeh and Morgan 1987), statistical aberration or violations in the assumptions of the mixed mating model (Ritland and El-kassaby 1985). Such violations which bias the estimates, among other factors, include spatial heterogeneity of the pollen gamete pool, segregation

distortion, assortative mating, differential selection intervening between the union of gametes and the point of census, and population subdivision.

Multilocus estimates of outcrossing rates (t_m) are robust to violations of model assumptions and therefore are generally considered to be more accurate than single-locus estimates (Ritland and Jain 1981). In all cases, t_m estimates were higher than average t_s estimates (Table 3.2), but they were not significantly different as determined by their means and standard errors. Similar observations were also found in wind-pollinated (e.g., Yeh and Morgan 1987; Xie et al. 1991) and animal-pollinated species (e.g., Godt and Hamrick 1991; Boshier et al. 1995). The average of single-locus estimates of outcrossing rates is expected to be lower than multilocus estimates when cross-pollination occurs among family members (Ritland and Jain 1981; Shaw et al. 1981). In addition multilocus estimates are not as sensitive to false assumptions that tend to depress single-locus estimates, and therefore come out higher. Most obviously, single-locus estimates cannot detect the difference between selfing and mating among related individuals nearly as efficiently as multilocus estimates.

Inter-population variation in outcrossing rates is common in plant species and could be attributed to differences among populations in genetic compositions and environmental conditions (Clegg 1980). Presence or absence of self-incompatibility mechanisms (Bawa et al. 1985; Murawski and Hamrick 1992a), availability of pollinators and their foraging behavior (Cruzan et al. 1994), density and distribution of flowering individuals (Murawski and Hamrick 1992b), and flower density and phenological variation (Hall et al. 1994) are among the factors that affect the mating system. In this study t_m and average t_s varied among populations and revealed a geographic pattern with

western populations exhibiting higher outcrossing rates than eastern populations (Table 3.2). This east-west pattern conforms to cluster analysis of the same 11 populations using Nei's genetic distance coefficients and UPGMA (Chapter 2). The low outcrossing rates of eastern populations could be attributed to greater habitat disturbance, low density and isolation of flowering mature trees. Low outcrossing rates in populations 9 and 10, where density was less than one flowering tree per hectare, and high outcrossing rates in population 7, where density was more than three flowering trees per hectare, could suggest that reduced population density associated with habitat disturbance reduced outcrossing.

The influence of density of flowering individuals on outcrossing rates has been reported for wind-pollinated conifers (Boyle et al. 1991) and animal-pollinated species (Hall et al. 1994; Boshier et al. 1995). Murawski et al. (1994) also discussed the importance of habitat disturbance to mating system. Density-dependent reproductive success, that is, the "Allee effect" (Allee and Rosenthal 1949) has been demonstrated for *Shorea siamensis*, a characteristic tree species of dry dipterocarp forest often in association with *P. macrocarpus*. Ghazoul et al. (1998) observed pollination success and seed set along a gradient of increasing disturbance in western Thailand. At high levels of disturbance, where densities of adult *S. siamensis* were reduced, there were significantly lower stigma pollen loads and seed set than in less disturbed, higher density sampling locations.

Individual tree outcrossing rates (t_{mi}) within populations would also affect population outcrossing rates (Figure 3.2). Eastern populations, where outcrossing rates were low, had a larger proportion of trees (>20%) with outcrossing rates less than 90%.

The extreme would be populations 9 and 10 where 43% and 73% of the trees, respectively, were outcrossed at less than 90% (Figure 3.2). Coefficients of variation also suggested that there was greater variation of individual tree outcrossing rates (t_{mi}) in eastern populations than in western populations (Figure 3.2). Such intra- and inter-population variation of outcrossing rates in *P. macrocarpus* is not surprising since genetic compositions of trees and habitat characteristics affecting the mating system (Clegg 1980) could be different both among and within populations. The large proportion of trees with more than 80% outcrossing (Figure 3.2) would suggest that abortion of inbred progeny would likely occur in *P. macrocarpus*. In addition, *P. macrocarpus* would also possess self-incompatibility mechanism which is a common characteristic of most tropical hermaphroditic species (Bawa et al. 1985).

Observed inbreeding coefficients in progeny populations (F_o) were generally greater than the expected inbreeding coefficients at equilibrium (Table 3.2), suggesting that progeny populations had more homozygotes than expected. The movement of pollinators among adjacent flowers within the crown or between adjacent crowns of related neighbours might be confined to short distances and this would increase inbreeding and selfing within populations (Levin and Kerster 1968). In contrast, all parental (adult) populations exhibited excess heterozygotes, as indicated by negative F_p values (Table 3.2). This might suggest that selection against homozygotes operated in the progeny populations throughout the life cycle. This allowed few selfed or inbred progenies to survive to the adult stage, resulting in more outcrossed adult trees.

Selection in favour of heterozygotes typically occurs in more extreme environments (Brown 1979). North-eastern Thailand tends to be much drier than the rest

of the country, with poorer soils, leading to more xeric conditions which might promote selection in favour of heterozygotes. In addition, north-eastern populations tend to be more heavily disturbed, such that seedlings of *P. macrocarpus* may be experiencing novel environments to which the species is not well adapted. In such circumstances, where reduced population size and increased inbreeding interacts with a lack of adaptation, the species may be entering one of the "extinction vortices" described by Gilpin and Soulé (1986) to describe the different combination of processes that may lead to extinction. This particular combination of circumstances is characteristic of Gilpin and Soulé's "A" vortex, in which reduced effective population size and increased inbreeding results in an increasing lack of adaptation. Even though there may be selection in favour of heterozygotes, there is simply insufficient genotypic diversity being generated to allow effective selection.

As Gilpin and Soulé (1986) point out, the "A" vortex has the longest time scale, and is not likely in itself to lead to extinction, but leaves the population much more susceptible to other processes leading to extinction. Options to improve the likelihood of survival of the species include measures to increase effective population size. These options may include planting, but the reduction of fragmentation by providing genetic "corridors" linking otherwise isolated populations is also possible. *P. macrocarpus* is a popular species for farmers to maintain, or potentially to plant in their fields (P. Vityakon, personal communication), and the contribution of trees in an agricultural landscape to conserving forest populations should not be neglected.

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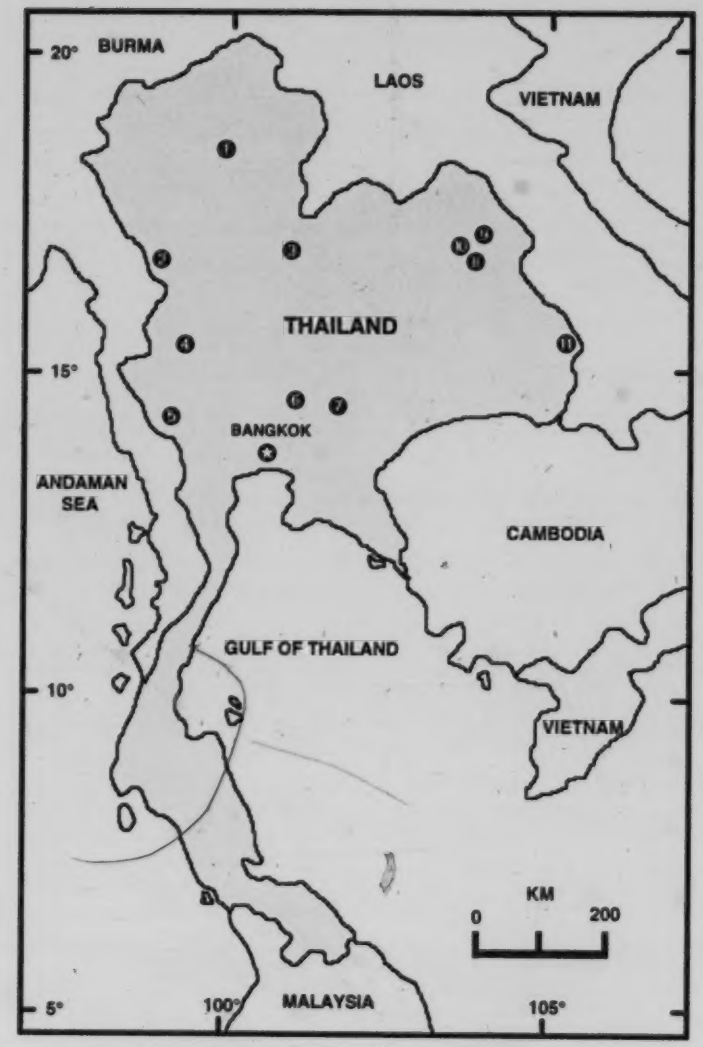

Figure 3.1 Map of Thailand showing locations of 11 sampled populations of *P. macrocarpus*.

Table 3.1 Geographic location, elevation, forest type, density and number of sampled trees of 11 populations of *P. macrocarpus*.

Population		Latitude (°N)	Longitude (°E)	Elevation (m)	Forest type [a]	Flowering tree density per hectare	No. of sampled trees
No.	Name						
1	Lampang [b]	18°35'	99°54'	350	MDF	2.9	15
2	Tak [b]	16°42'	98°57'	600	MDF	3.1	15
3	Pitsanulok [b]	16°50'	100°53'	500	MDF	2.7	15
4	Uthaithani [b]	15°30'	99°22'	220	DDF	3.2	34
5	Kanchanaburi [b]	14°15'	99°10'	500	MDF	2.6	13
6	Saraburi [c]	14°35'	101°12'	200	MDF	2.1	33
7	Sakaerat [b]	14°25'	101°45'	380	DDF	3.8	95
8	Phuphan-1 [c]	16°48'	103°53'	480	HGF	1.5	12
9	Phuphan-2 [c]	17°02'	103°57'	240	DDF	0.3	7
10	Phuphan-3 [c]	16°58'	103°45'	310	DDF	0.8	15
11	Khong-chiam [c]	15°24'	105°29'	200	DDF	1.4	15

[a] MDF: mixed deciduous forest (moist site); DDF: dry dipterocarp forest (dry site); HGF: hill evergreen forest (moist site).
[b] Less disturbance.
[c] Greater disturbance.

Table 3.2 · Single-locus (t_s) and multilocus (t_m) outcrossing rates and inbreeding coefficient of parental (F_p) and progeny (F_o) populations and at equilibrium (F_e) of 11 populations of *P. macrocarpus* (standard errors in parentheses).

	Population										
Locus	1	2	3	4	5	6	7	8	9	10	11
AAT-1	0.911 (0.121)	0.914 (0.070)	-	0.698 (0.085)	0.902 (0.081)	0.909 (0.065)	0.823 (0.037)	0.711 (0.107)	0.979 (0.180)	0.905 (0.092)	0.812 (0.089)
AAT-2	0.827 (0.065)	0.912 (0.116)	0.922 (0.092)	0.877 (0.060)	0.860 (0.064)	0.917 (0.046)	0.849 (0.035)	0.927 (0.095)	0.624 (0.101)	0.508 (0.100)	0.893 (0.085)
AAT-3	0.978 (0.097)	0.794 (0.128)	0.939 (0.087)	0.924 (0.084)	0.724 (0.135)	0.743 (0.075)	0.920 (0.039)	0.860 (0.069)	0.742 (0.121)	0.499 (0.126)	-
ADH	-	-	-	0.922 (0.107)	-	-	-	-	-	-	-
APH-2	0.937 (0.064)	0.898 (0.163)	0.882 (0.081)	0.953 (0.088)	0.846 (0.092)	-	0.858 (0.047)	0.981 (0.125)	0.926 (0.170)	0.956 (0.077)	0.490 (0.149)
EST	0.883 (0.131)	0.956 (0.086)	0.740 (0.091)	0.504 (0.000)	0.857 (0.000)	0.564 (0.050)	0.761 (0.047)	0.474 (0.081)	0.793 (0.108)	0.484 (0.096)	0.798 (0.083)
IDH	-	0.984 (0.095)	0.835 (0.143)	0.784 (0.084)	0.827 (0.110)	0.505 (0.111)	-	0.811 (0.182)	-	0.636 (0.136)	0.963 (0.000)
PGI-2	-	-	0.921 (0.665)	0.962 (0.061)	-	0.925 (0.128)	0.785 (0.047)	0.981 (0.398)	0.739 (0.218)	0.772 (0.122)	0.690 (0.073)
PGM-2	-	-	-	-	-	-	0.920 (0.069)	-	-	-	0.709 (0.150)
MDH-1	0.994 (0.818)	0.988 (0.277)	-	0.972 (0.279)	0.999 (0.160)	-	-	-	-	-	-

Table 3.2 Continued.

	Population										
Locus	1	2	3	4	5	6	7	8	9	10	11
MDH-2	-	0.949 (0.546)	-	-	0.609 (0.000)	-	-	-	-	-	-
ME-2	0.954 (0.058)	0.920 (0.100)	0.931 (0.079)	0.913 (0.178)	0.940 (0.083)	0.855 (0.085)	0.925 (0.048)	0.579 (0.105)	0.021 (0.000)	0.499 (0.068)	0.957 (0.120)
MR-3	0.905 (0.270)	0.992 (0.144)	0.966 (0.151)	0.983 (0.091)	0.995 (0.087)	0.854 (0.100)	0.992 (0.057)	0.962 (0.155)	0.133 (0.000)	0.978 (0.117)	0.649 (0.128)
6PG-1	0.907 (0.082)	0.956 (0.237)	0.879 (0.066)	0.950 (0.061)	0.777 (0.160)	0.870 (0.080)	0.797 (0.064)	-	0.506 (0.111)	-	0.770 (0.136)
6PG-2	0.941 (0.096)	0.986 (0.116)	0.986 (0.095)	0.975 (0.069)	0.728 (0.111)	0.853 (0.066)	0.970 (0.038)	0.877 (0.148)	0.931 (0.130)	0.635 (0.089)	0.559 (0.094)
6PG-3	0.961 (0.072)	0.856 (0.189)	0.957 (0.192)	0.921 (0.065)	0.910 (0.081)	0.904 (0.000)	0.861 (0.053)	0.928 (0.000)	-	0.271 (0.159)	0.906 (0.144)
Mean t_s	0.927 (0.047)	0.931 (0.058)	0.905 (0.070)	0.881 (0.134)	0.844 (0.112)	0.809 (0.145)	0.872 (0.074)	0.826 (0.170)	0.620 (0.317)	0.649 (0.228)	0.746 (0.178)
t_m	0.945* (0.022)	0.958 (0.027)	0.959 (0.021)	0.953* (0.015)	0.949 (0.026)	0.898* (0.019)	0.947* (0.010)	0.891* (0.032)	0.719* (0.045)	0.751* (0.032)	0.895* (0.029)
F_p	-0.212	-0.318	-0.316	-0.316	-0.152	-0.228	-0.312	-0.275	-0.315	-0.457	-0.329
F_o	-0.010	0.001	0.042	0.090	0.033	0.108	0.048	0.103	0.305	0.144	0.219
F_e	0.028	0.021	0.021	0.024	0.026	0.054	0.027	0.058	0.163	0.142	0.055

* Significant less than 1 (i.e., $[t + 2\,SE] < 1$).

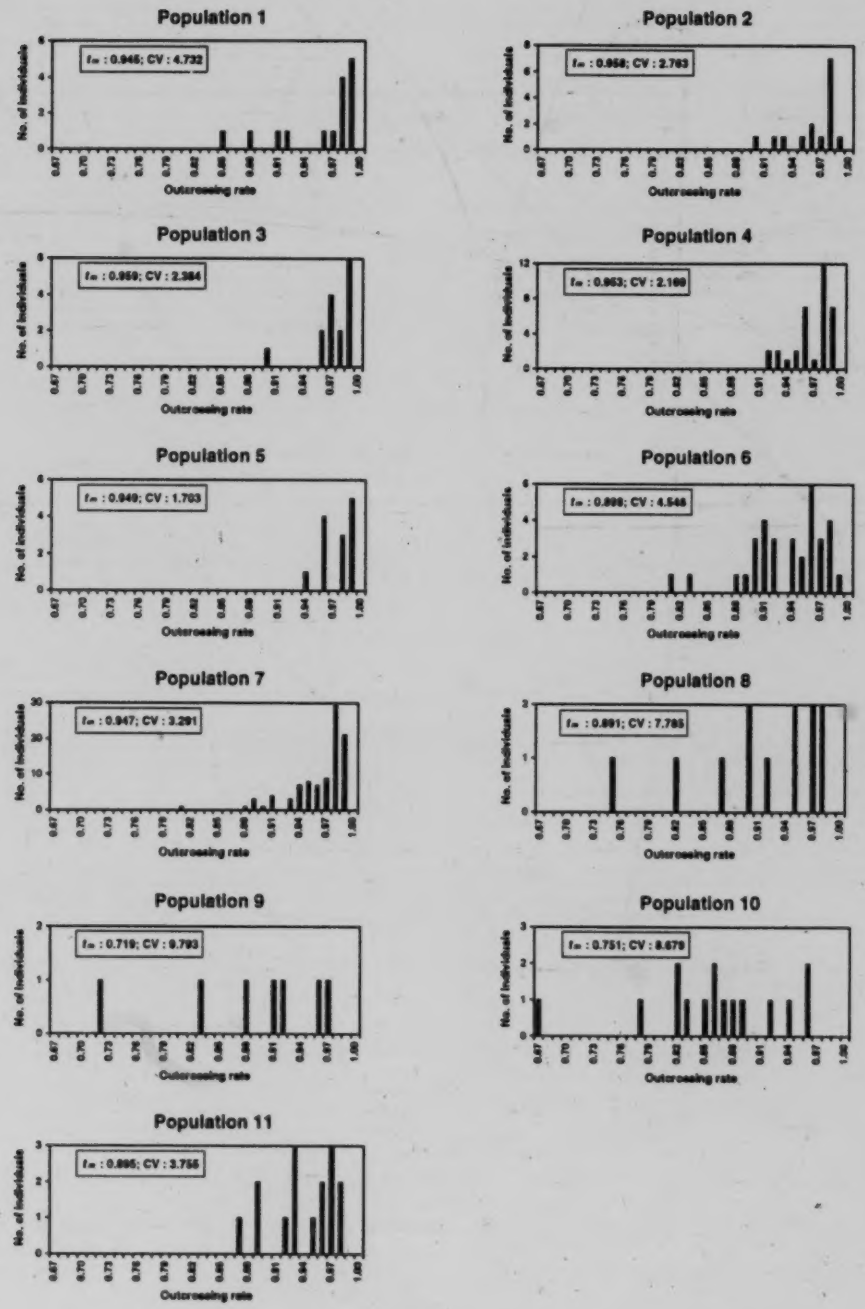

Figure 3.2 Distribution of individual-tree outcrossing rates and coefficients of variation (CV) in each of 11 populations of *P. macrocarpus* (value on the x-axis starts at the lowest outcrossing rate detected).

CHAPTER 4

GENETIC VARIATION IN GROWTH, MORPHOLOGICAL AND PHYSIOLOGICAL TRAITS IN *PTEROCARPUS MACROCARPUS* SEEDLINGS GROWN IN NURSERY

4.1 Introduction

Knowledge of genetic variation patterns of a species is fundamental to the success of its genetic improvement which basically is the exploitation of genetic variation. Patterns of genetic variation can be detected at both population and within-population levels (e.g., Yeh and Rasmussen 1985; Hamrick et al. 1992; Xie and Ying 1996). The information is useful to determine strategies for selection of parent trees. For instance, when the level of variation among populations is large relative to the level of variation within a population, the selection of parent trees should emphasize the population level and less effort should be devoted to selection within populations. Genetic variation and degree of genetic control also vary among traits, ages and environments (e.g., Cotterill and Dean 1988; Bouvet and Vigneron 1995; Mullin et al. 1995; Paul et al. 1997; Wu et al. 1995; Xie and Ying 1996). Cornelius (1994) compiled, from 67 published papers, estimates of individual tree narrow-sense heritability and additive genetic coefficient of variation of seven traits of forest trees. Those estimates were of growth, morphological and structural traits obtained mainly from conifers and some broadleaf trees.

Physiology, on the other hand, has limited contribution to forestry partly because of a lack of communication between field and laboratory workers and partly because of a lack of a general understanding of the role of physiology in forestry (Kramer 1986). The

physiological processes of trees are the machinery through which the genetic potential and the environment operate to determine the quantity and quality of growth. Only recently, genetic variation in physiological traits has been documented for forest tree species (e.g., Zhang et al. 1993; Dang et al. 1994; Aitken et al. 1995; Major and Johnsen 1996). Attempts were also made to investigate the potential use of physiological traits as markers for early selection but has met with limited success although the potential exists (Larsen and Wellendorf 1990; Greenwood and Volkaert 1992; Sulzer et al. 1993).

Pterocarpus macrocarpus Kurz is an important leguminous tree species of southeast Asia. Its natural distribution extends from Burma through Thailand and Laos to southern Vietnam (Rojo 1977). It is economically important to Thailand. It is used extensively in reforestation programs because it is relatively easy to grow in the nursery. *P. macrocarpus* also generally produces abundant fruit crops that would ensure adequate seed supply for planting stock production. Isozyme analysis has revealed high levels of genetic diversity and a high degree of among-population differentiation with an east-west pattern of population grouping (Chapter 2). Despite its commercial and operational plantation importance, breeding programs have not yet been initiated in Thailand. Although provenance trials have been recently established by ASEAN Forest Tree Seed Centre Project, Thailand, they are still too young to provide any useful information.

Nursery trials provide a means to test and screen a large number of seedlings and families for superiority in growth at a reasonably low cost and within a short period of time. Measurements of a large number of traits from a large number of seedlings can be accomplished within a limited time period. Nursery trials also facilitate the analysis of traits that are difficult to measure in the field such as some physiological traits, biomass,

etc. Although change in growth behaviour due to maturation could result in weakening the age-age correlation of traits that were measured between nursery and field growth (Cannell et al. 1978; Greenwood and Volkaert 1992), evaluation of seedlings in the nursery enables rogueing of very poor families prior to establishing long term field trials. In this study, seedlings from a total of 112 families from six populations of *P. macrocarpus* sampled from Thailand were assessed for their growth, morphological and physiological traits under nursery conditions in Thailand. The objectives were (1) to examine the level of genetic variation and (2) to determine the magnitude of genetic control and genetic relationship among these traits.

4.2 Materials and methods

4.2.1 Plant materials and experimental design and establishment

Open-pollinated *P. macrocarpus* seeds of 112 families from six populations collected from Thailand were used in this study (Figure 4.1). These families were subsets of 287 families from 11 populations used for an isozyme variation study (Chapter 2). Details of geographic locations, climate, forest types, inbreeding coefficient (F), multilocus outcrossing rate (t_m), and number of families for each of six populations are presented in Table 4.1. Eighty seeds from each of 112 families were individually weighed and seed weight was recorded for each individual seed. Seeds were scarified with medium grain sand paper in order to eliminate seedcoat dormancy and enhance rapid and uniform germination (Liengsiri 1987). A 24-cell multipot tray was used for seed germination and early seedling growth. The size of each cell was 2 inches in diameter and 4 inches in depth with an approximate volume of 190 ml. A single seed was sown into

each cell. The planting medium was a mixture of coconut husk fibre, sand and compost in a 2:1:1 ratio with pH 7.5. Multipot trays were arranged by family for ease of operation. Seeds were sown in late May 1994. Germination was completed within 10 days after sowing. Germinants for each family were counted two weeks after sowing and germination percentage for each family was calculated (Appendix 1). At this stage, all germinants possessed tiny true leaves. Approximately 0.5 g of 2-month formula controlled release fertilizer (Osmocote 13-13-13) was applied for each seedling three weeks after sowing. Seedlings were raised for 12 weeks before being transplanted into larger pots.

Sixteen healthy seedlings from each of 112 families were randomly selected and each seedling was transplanted into a 3-liter volume clay-pot (7-inch diameter and 8-inch depth) filled with the same mixture of planting medium used for germination and early growth. A total of 1,792 seedlings derived from 112 families were transplanted. The arrangement of pots was a randomized complete block design with 16 replications of single-tree plots. Spacing between adjacent seedlings was approximately eight inches. Seedlings were raised for a total period of 30 weeks after sowing.

During the course of seedling growth, water was regularly supplied every second day to maintain adequate soil moisture. An additional 10 g of 2-month formula controlled release fertilizer (Osmocote 13-13-13) was also supplied for each seedling at week 12 and week 21 during a 30-week growth period. Nursery conditions were, on average, 27°C, 80% RH, and 680 μmol m^{-2} s^{-1} light intensity (photosynthetic active radiation, PAR).

4.2.2 Measurement and data collection

4.2.2.1 Growth and morphological traits

Height growth measurement commenced at week 3 after sowing and continued every 3-weeks over a 30-week growth period. A total of 10 measurements were made. Diameter growth at root collar was measured when seedlings were 12 weeks old and measurements were continued every 3-weeks over a 30-week growth period. A total of seven measurements were made.

Biomass (dry weight) traits were assessed at the end of the 30-week growth period in mid December 1994. Individual seedlings were harvested, washed, separated into parts, i.e., leaf, stem, taproot and fibrous root, and oven dried at 80°C for 24 hours. The dry weight of each component of plant parts was recorded for each seedling. Specific leaf weight (leaf weight per unit leaf area) was also determined for each seedling. Four leaves from each seedling were sampled and measured for surface area using a portable area meter (leaf area meter model CI-202, CID, Inc., USA) prior to oven drying and weighing.

4.2.2.2 Physiological traits

Physiological traits (gas exchange) including net photosynthesis (A), transpiration (E) and water-use efficiency (WUE) were measured in late November 1994 when seedlings were 27 weeks old. Net photosynthesis and transpiration were simultaneously measured using an infrared gas analyzer (IRGA) (Photosynthesis System model CI-301, CID, Inc., USA). Water-use efficiency (WUE) was determined from A and E, where WUE = A/E (Sinclair et al. 1984). Only five replications were included for gas exchange measurements. Two mature and fully expanded leaves from each seedling were randomly

assigned for measurements. Physiological measurements were conducted under full sunlight during the time period 8:30-15:30. During the measurements, the average temperature was 31°C ranging from 25°C to 34°C whereas the average PAR was 1,660 μmol m^{-2} s^{-1} ranging from 1,026 to 2,090 μmol m^{-2} s^{-1}. Although photosynthesis at light saturation of *P. macrocarpus* has not yet been reported, light intensity (PAR) was considered adequate to obtain maximum photosynthetic rate at light saturation (Limpiyaprapant 1993). Each physiological measurement was conducted for 30 seconds inside a 1-liter closed system CID leaf chamber. The sequence of measurements within each replication was random.

Details of growth, diameter, biomass (dry weight) and physiological traits are described in Table 4.2.

4.2.3 Statistical and genetic analysis

4.2.3.1 Growth and morphological traits

Analysis of variance and covariance was conducted for height, diameter and biomass traits using the following linear model:

$$Y_{ijk} = \mu + R_i + P_j + RP_{ij} + F_k(P_j) + E_{ijk} \quad (1)$$

where

μ - grand mean

R_i - i^{th} replication effect, i = 1-16

P_j - j^{th} population effect, j = 1-6

RP_{ij} - effect of replication-by-population interaction

$F_k(P_j)$ - k^{th} family effect within the j^{th} population, k = 1, 2, ..., n (n ranges from 13 to 27)

E_{ijk} - residual error

All effects in the model were assumed to be random. Expected mean squares (EMS) and expected mean cross products (EMCP) were estimated using SAS varcomp type I (SAS Institute Inc., Cary, NC). The structure of analysis of variance and covariance is presented in Table 4.3. Significance tests of effects in the model followed Satterthwait's approximate test procedure (1946).

Due to a certain degree of inbreeding (Squillace 1974) (see inbreeding coefficient (*F*), Table 4.1), family variance is assumed to estimate one-third of the additive genetic variance. Narrow-sense heritabilities for individuals and families were computed as:

$$\text{Individual heritability, } h_i^2 = \frac{3 \times \sigma_{f(p)}^2}{\sigma_e^2 + \sigma_{f(p)}^2} \qquad (2)$$

$$\text{Family heritability, } h_f^2 = \frac{\sigma_{f(p)}^2}{\sigma_e^2 / k_{10} + \sigma_{f(p)}^2} \qquad (3)$$

Descriptions of terms above are given in Table 4.3. Standard errors of the heritabilities were estimated using the formula given by Nyquist (1991).

Genetic correlation (r_g) between traits was calculated following Falconer (1989):

$$r_g = \frac{COV_f(x,y)}{\sqrt{\sigma_{fx}^2 \sigma_{fy}^2}} \qquad (4)$$

Where $COV_f(x,y)$ is family covariance between traits X and Y, and σ_{fx}^2 and σ_{fy}^2 are their corresponding family (i.e., family-within-population) variances. Standard error of genetic correlation was estimated following Robertson (1959).

4.2.3.2 Physiological traits

Analysis of variance and covariance for physiological traits was conducted using the following linear model:

$$Y_{ijkl} = \mu + R_i + P_j + RP_{ij} + F_k(P_j) + L_l(FP_{jk}) + E_{ijkl} \quad (5)$$

where

μ - grand mean

R_i - i^{th} replication effect, i = 1-5

P_j - j^{th} population effect, j = 1-6

RP_{ij} - effect of replication-by-population interaction

$F_k(P_j)$ - k^{th} family effect within the j^{th} population, k = 1, 2, …, n (n ranges from 13 to 27)

$L_l(FP_{jk})$ - l^{th} leaf effect within the k^{th} family within the j^{th} population, l = 1-2

E_{ijkl} - residual error

All effects in the model were assumed to be random. Expected mean squares (EMS) and expected mean cross products (EMCP) were estimated using SAS varcomp type I (SAS Institute Inc., Cary, NC). The structure of the analysis of variance and covariance is presented in Table 4.4. Significance tests of effects in the model followed Satterthwait's approximate test procedure (1946).

Similar to growth and morphological traits, the narrow-sense heritabilities for individual and family were computed as:

$$\text{Individual heritability, } h_i^2 = \frac{3 \times \sigma^2_{f(p)}}{\sigma^2_e + \sigma^2_{l(fp)} + \sigma^2_{f(p)}} \quad (6)$$

$$\text{Family heritability, } h_f^2 = \frac{\sigma^2_{f(p)}}{\sigma^2_e/k_{14} + k_{13}\sigma^2_{l(fp)}/k_{14} + \sigma^2_{f(p)}} \qquad (7)$$

Descriptions of terms above were given in Table 4.4. Standard errors of the heritabilities were estimated using the formula given by Nyquist (1991).

Genetic correlation (r_g) between traits was calculated using equation (4) and standard error was calculated following Robertson (1959).

4.3 Results

The average percentage of seedling survival following the 30-week growth period was 95% and the range was from 92% to 97% among populations and from 75% to 100% among families (Table 4.5). However, there was no significant difference among populations for seedling survival after the 30-week growth period.

4.3.1 Growth and morphological traits

Population means and their standard deviations, ranges of family means, grand means and coefficients of variation for seedling height growth are presented in Table 4.6. Rapid height growth as revealed by grand means occurred during weeks 6 to 18 and gradually declined toward the end of growth period. Coefficients of variation (C.V.) gradually increased as age advanced indicating that variation increased with age. After the 30-week growth period, population 5 had the largest average height growth at 40.9 cm which was 13% larger than the grand mean (36.2 cm) whereas population 1 had the smallest height growth averaging 29.8 cm which was 17% smaller than grand mean (Table 4.6). There was 27% difference in mean height growth between populations 1 and

5 although both were sampled from mixed deciduous forest but from very different geographic locations (Table 4.1).

Diameter revealed a somewhat consistent rate of growth during the growth period (Table 4.7), although a slightly higher growth rate was observed at younger seedling age. Coefficients of variation (C.V.) indicated that relative to height there was less variation in diameter growth among the seedlings and among the ages although they slightly increased with age (Table 4.7). Similarly to height growth, population 5 had the largest diameter growth while population 1 remained the smallest after the 30-week growth period (Table 4.7). Average diameter growth of population 5 (11.04 mm) was 6% larger than the grand mean (10.38 mm) and was 11% larger than that of population 1 (9.76 mm) which was approximately 6% smaller than the grand mean (Table 4.7).

Table 4.8 presents population means and standard deviation, ranges of family means, grand means and coefficients of variation (C.V.) for the biomass (dry weight) traits. As revealed by the grand means, total biomass was partitioned more to the shoot than to the root, averaging 6.281 g and 5.094 g, respectively. As a result, the shoot-to-root ratio (S:R) at 1.354 was greater than 1.0. Shoot biomass was allocated equally to leaf (3.027 g) and to stem (3.254 g). In contrast, the allocation of root biomass to taproot was approximately 2.8 times more than that to the fibrous root, averaging 3.748 g and 1.356 g, respectively. Coefficients of variation among the biomass traits were similar among each other but they were, generally, approximately two to three times larger than those of height and diameter, respectively (Tables 4.6, 4.7 and 4.8). The exception was specific leaf weight (SLWT) with the smallest coefficient of variation which implied less variation among the seedlings for this trait (Tables 4.6, 4.7 and 4.8).

Plant biomass among populations also exhibited a similar pattern to that of height and diameter growth. Population 5 had the largest total dry weight (14.429 g) whereas population 1 had the smallest total dry weight (8.741 g) (Table 4.8). Total dry weight of population 5 was 26% larger than the grand mean (11.375 g) and was 39% larger than that of population 1 whose mean was 23% smaller than the grand mean. Similarly, this pattern was also observed in biomass measurements for most of the other individual plant parts (Table 4.8). Family means within populations and standard deviations for all height, diameter and biomass traits are also presented in Appendices 2 to 27.

Analysis of variance for height growth (Table 4.10) showed that population and family-within-population effects were highly significant at 1% probability level for all measurements. Replication effect was not significant at the early measurements but was highly significant, at 1% probability level, from H12 to H30. There was no significant replication-by-population effect for all height traits. The percentage of total variance due to the replication effect was low at early ages and increased with the age of the seedlings. The percentage of total variance due to family-within-population effect, on the other hand, was high at early ages but decreased with the age of seedlings and was relatively stable, at 13%, toward the end of the growth period. The population effect was relatively stable throughout the growth period. The contribution to total variance from the family-within-population effect was larger than that from replication and population effects at early measurements but was similar to the replication and population effects at the later measurements. The residual effect at 53% to 69% explained the greatest proportion of the total variance (Table 4.10).

Analysis of variance for diameter growth (Table 4.11) also exhibited a similar pattern to that of height growth. The population effect was significant at either 1% or 5% probability level while the family-within-population effect was highly significant at 1% probability level for all diameter measurements. The replication effect was highly significant at 1% probability level only at the older ages. The replication-by-population effect was not significant for almost all diameter measurements except for D18 which was significant at the 5% probability level but its percentage of total variance was relatively small (Table 4.11). The percentage of total variance due to replication and population effects was relatively small with its maximum value of less than 5%. In contrast, the contribution to total variance from the family-within-population effect was relatively large compared to that from replication and population effects, ranging from 16% to 21%. The residual effect explained the greatest proportion of the total variance, ranging from 72% to 78%, indicating large variation among the seedlings.

Analysis of variance for biomass traits (Table 4.12) revealed high significance at the 1% probability level for replication, population and family-within-population effects whereas the replication-by-population effect was nonsignificant. Generally, the percentage of total variance due to the family-within-population effect was slightly larger than that of the replication and population effects for most biomass traits except specific leaf weight (SLWT) for which the replication effect was approximately five times larger than the population and family-with-population effects (Table 4.12). The residual effect remained the largest proportion of the total variance for all biomass traits as was observed for the height and diameter growth.

Estimates of individual and family heritabilities for height growth were moderate to high ranging from 0.494 (±0.078) to 1.00 (±0.11) and from 0.744 (±0.036) to 0.895 (±0.015), respectively (Table 4.14). Both individual and family heritabilities declined with the ages of seedlings and they coincided with the decline in the family variance (Table 4.10). However, the heritability estimates were relatively stable at the older seedling ages. Standard errors for heritability were small relative to the size of the heritability estimates (Table 4.14).

Diameter growth also had high heritability ranging from 0.549 (±0.083) to 0.680 (±0.092) for individual estimates and from 0.768 (±0.033) to 0.812 (±0.026) for family estimates (Table 4.14). Standard errors for both heritability estimates were also relatively small. On average, family heritability was approximately 32% larger than the individual heritability. There was no age trend observed for heritability estimates in diameter growth. All estimates were relatively stable over seedling ages.

There was variable magnitude of heritability estimates for the biomass traits (Table 4.14). Except for S:R and SLWT, all other biomass traits had moderate individual heritabilities ranging from 0.386 (±0.069) for FROOT to 0.564 (±0.084) for STEM. Family heritabilities were higher, ranging from 0.686 (±0.044) for FROOT to 0.774 (±0.032) for STEM. SLWT had the lowest individual heritability (0.094 ± 0.04) among all biomass traits investigated. Its family heritability (0.324 ± 0.095) was approximately three times larger. S:R biomass was another trait with low individual heritability (0.291 ± 0.068) but its family heritability (0.614 ± 0.054) was comparable to that of the other biomass traits. Standard errors for these estimates were also relatively small as observed in the other growth traits (Table 4.14).

Genetic correlations among height growth at different ages varied from moderate to almost perfect values, ranging from 0.394 (±0.105) to 0.997 (±0.001), and most of the estimates were larger than 0.7 (Table 4.15). Generally, correlations declined as the interval between two height measurements increased. Among all height measurements, H3 seemed to have lower correlations with the other height measurements when compared to height at the older seedling ages. Standard errors were relatively small and were mostly less than 10% relative to the size of their corresponding correlation estimates.

Genetic correlations between height and diameter traits were moderate to high, ranging from 0.546 (±0.089) to 0.917 (±0.032), with the majority of the estimates being greater than 0.7 (Table 4.16). Standard errors were small relative to their corresponding estimates. Except TROOT for which correlations remained relatively stable with all height measurements, correlations between height and biomass traits generally increased with the age of seedlings, though slightly decreasing toward the end of growth period (Table 4.16). A weak correlation was observed between H3 and LEAF (0.297 ± 0.116) whereas all other estimates were moderate to high, varying from 0.401 (±0.11) to 0.892 (±0.034). Generally, height exhibited a better correlation with shoot (above ground part) than with root (under ground part) biomass. Within the shoot portion, height was correlated more closely with stem than with leaf biomass. Standard errors were small relative to the estimates except for traits S:R and SLWT that were weakly correlated with height (Table 4.16).

There were high to perfect correlations among the diameter growth at different seedling ages, ranging from 0.857 (±0.046) to 1.00 (±0.006), with most estimates being

greater than 0.9 (Table 4.17). Standard errors associated with the estimates were also small and the largest standard error was only 5% of its corresponding correlation estimate. Similarly to height growth, correlations of diameter growth also declined as the interval between two measurements increased. Genetic correlations between diameter and biomass traits were moderate to high, ranging from 0.436 (±0.106) to 0.892 (±0.032) with most estimates being larger than 0.6 (Table 4.18). Standard errors associated with the correlation estimates remained small. Similarly to height growth, diameter growth also exhibited a better correlation with shoot than with root biomass. It also correlated better with stem than with leaf biomass. Diameter was not or only weakly correlated with S:R and SLWT and the estimates had relatively large standard errors (Table 4.18).

There were moderate to high genetic correlations associated with relatively small standard errors observed among the biomass traits, ranging from 0.663 (±0.079) to 0.980 (±0.006) and with the majority of the estimates larger than 0.8 (Table 4.19). The genetic correlation between LEAF and STEM (0.852 ± 0.039) was larger than that observed between TROOT and FROOT (0.663 ± 0.079). S:R had low correlation with the above ground biomass traits (i.e., LEAF, STEM and SHOOT) but had either weak or negative correlation with the under ground biomass traits (i.e., TROOT, FROOT and ROOT). A weak correlation was also observed between S:R and TOTAL biomass. Similarly, SLWT was not correlated with the biomass traits. There was, however, a moderate correlation between S:R and SLWT (0.462 ± 0.215) (Table 4.19). Standard errors of correlations between S:R and SLWT and other biomass traits were relatively large (Table 4.19).

4.3.2 Physiological traits

The average net photosynthesis (*A*), transpiration (*E*) and water-use efficiency (WUE) of *P. macrocarpus* seedlings were 8.39 μmol m^{-2} s^{-1}, 1.4 mmol m^{-2} s^{-1} and 6.56 μmol CO_2 /mmol H_2O, respectively (Table 4.9). These physiological traits also exhibited large variation among the seedlings as indicated by the large coefficients of variation (Table 4.9). As was observed in height, diameter and biomass traits, population 5 had the highest *A*, averaging 9.08 μmol m^{-2} s^{-1}, which was approximately 8% higher than the grand mean (8.39 μmol m^{-2} s^{-1}). Although population 1 did not display the lowest *A*, as was observed for height, diameter and biomass traits, its photosynthesis remained low (7.98 μmol m^{-2} s^{-1}) and was only 1.3% higher than the lowest rate (7.88 μmol m^{-2} s^{-1}), found in population 3 (Table 4.9). In contrast to low photosynthesis, transpiration of population 1 was the highest (1.49 mmol m^{-2} s^{-1}). Population 3, however, maintained the lowest *E* at 1.31 mmol m^{-2} s^{-1}.

Population 5, as a result of having the highest *A* and low *E*, maintained the highest WUE at 7.28 μmol CO_2 /mmol H_2O which was approximately 11% higher than the grand mean (6.56 μmol CO_2 /mmol H_2O). Population 1, on the other hand, having low *A* and the highest *E* also displayed the lowest WUE (5.82 μmol CO_2 /mmol H_2O). Water-use efficiency between these two populations differed by approximately 20% (Table 4.9).

Family means within populations and standard deviations for physiological traits are also presented in Appendices 28 to 30.

Analyses of variance for physiological traits are presented in Table 4.13. The family effect was highly significant at 1% probability level for all traits whereas the level

of significance for other effects varied among traits. The replication effect was not significant for *A* but was highly significant, at 1% probability level, for *E* and WUE. The population effect was highly significant, at 1% probability, only for WUE. The replication-by-population effect was significant at the 1% and 5% probability level for *A* and *E*, respectively and was not significant for WUE. The difference among sampled leaves within seedlings was not significant for all three physiological traits. As previously observed in other growth and biomass traits, the residual effect, at 75% to 83%, remained the largest proportion of the total variance in all three physiological traits (Table 4.13).

Estimates of heritabilities for the physiological traits were low to moderate, ranging from 0.256 (±0.079) to 0.428 (±0.092) for individual heritabilities and from 0.473 (±0.10) to 0.615 (±0.073) for family heritabilities (Table 4.14). Among the three physiological traits, WUE and *E* had the lowest and the highest heritability estimates, respectively. Standard errors relative to the size of their corresponding heritabilities ranged from 21% to 29% for individual heritabilities and from 11% to 21% for family heritabilities (Table 4.14). They were generally larger than those observed in other growth and most biomass traits (Table 4.14).

Genetic correlations among physiological traits are presented in Table 4.20. Photosynthesis was strongly correlated with transpiration but was weakly correlated with water-use efficiency. Transpiration, on the other hand, was moderately and negatively correlated with water-use efficiency. Generally, *A*, *E* and WUE were not correlated or only weakly correlated with the growth and biomass traits and their standard errors associated with the estimates were relatively large (Table 4.21). Among these three physiological traits, WUE exhibited slightly larger genetic correlations with the growth

and biomass traits than did *A* and *E* although the correlation estimates remained weak with large standard errors (Table 4.21).

4.4 Discussion

Sampled populations of *P. macrocarpus* exhibited high survival rate under nursery conditions with an overall mean of 95% and ranging from 75% to 100% among the populations (Table 4.5). High survival rate of seedlings in this study implied that the growth conditions in nursery were optimal and under such conditions seedlings would express their inherent genetic variation at an earlier age (Bongarten and Hanover 1985). The investigation of genetic variation in growth, morphological and physiological traits at the seedling stage would provide some useful information and opportunity for genetic management in *P. macrocarpus*.

4.4.1 Growth and morphological traits

After the 30-week growth period, the average growth performance of *P. macrocarpus* seedlings was 36.2 cm for height, 10.38 mm for diameter and 11.375 g for total biomass (Tables 4.6, 4.7 and 4.8). It was evident from the overall means that rapid height growth occurred between week 6 to week 18 (Table 4.6). Because seedlings were transplanted at week 12, the decreased rate of height growth observed at week 15 was possibly due to the impact of transplanting (Namkoong and Conkle 1976; Camussi et al. 1995). The decline in height growth toward the end of growth period starting at H24 would correspond to the approach of the end of regular growing season in Thailand. January to mid March is the dormant period of *P. macrocarpus* and the tree is leafless.

Diameter growth was also high during the early growth period and maintained a relatively stable growth rate throughout the growth season, although a slight decline was also observed at the end of growth period (Table 4.7). This would imply that diameter growth in *P. macrocarpus* was somewhat less sensitive to the approach of the dormant season than height growth. Boltz et al. (1986) also observed diameter growth continued while height growth declined near the end of growing season in loblolly pine seedlings. The slight decline toward the end of growth period was probably due to the increased competition between seedlings since diameter growth is sensitive to spacing (Xie et al. 1995).

The allocation of total biomass to shoot and to root varied among populations and appeared to be random for both mixed deciduous forest and dry dipterocarp forest (Tables 4.1 and 4.8). On average, the allocation of total biomass (11.375 g) to shoot (6.281 g) was approximately 10% higher than that to root (5.094 g) (Table 4.8). Among seedling part biomass, taproot (TROOT) was the largest part of total biomass and was approximately 2.8 fold larger than the fibrous root (FROOT). This might indicate that TROOT played major role as structural and food reserve tissue in *P. macrocarpus* seedlings. At time of biomass assessment, which was in mid December, both height and diameter growth at week 30 declined as the annual dormant period approached (January to mid March). During the dormant season, *P. macrocarpus* seedlings are leafless. The function of fibrous root for water and nutrient uptake would be expected to be minimal, since no further growth would continue during the dormant period. Thus, the allocation of total biomass to fibrous root would be minimized while a larger proportion of root biomass would be allocated to taproot as energy reserves for the following season's growth. This

would be crucial for seedling survival in *P. macrocarpus*. Inability to regenerate a root system rapidly increases the mortality of seedlings from drought or other factors (Krueger and Trappe 1967).

Mean height, diameter and biomass traits were different among sampled populations (Tables 4.6, 4.7, and 4.8). After the 30-week growth period, population 5 was the largest for height, diameter and total biomass while population 1 was the smallest for all these traits. Both populations were sampled from mixed deciduous forest from different regions (Table 4.1) but were grown in an environment that was similar to that of population 5. Populations 4 and 6 were located near population 5 and presumably were not much different in their environments, and they also exhibited superior growth performance (Tables 4.6, 4.7 and 4.8). Thus, the environment of the seed origin might have affected growth performance between populations. The influence of the environment of the origin was also reported in seed germination capacity in *P. macrocarpus* (Liengsiri 1987).

Genetic variation in growth and biomass traits in *P. macrocarpus* seedlings can be detected at an early age. Population and family-within-population effects were significant for all height, diameter and biomass traits (Tables 4.10, 4.11 and 4.12). The variance patterns were similar to those reported in earlier studies of young trees (e.g., Yeh and Rasmussen 1985; Fries and Lindgren 1986; Wu et al. 1995). Although replication, population and family-within-population effects were the significant sources of variation for all growth and biomass traits, the largest percentage of variation was due to differences among seedlings within families (Tables 4.10, 4.11, and 4.12). As an outcrossing species (Chapter 3), variation among seedlings in open-pollinated families

probably is indicative of the large number of effective pollen parents and the maintenance of considerable genetic variation in *P. macrocarpus*.

Significant replication effects (Tables 4.10, 4.11 and 4.12) were expected because of the single-tree design and genetic heterogeneity among the open-pollinated seedlings. In addition, within-nursery heterogeneity in microclimate and different times of transplanting among replications would also have contributed to the significant replication effect.

The population effect was significant for all growth and biomass traits (Tables 4.10, 4.11, and 4.12). This finding corroborated with that of isozyme analysis (Chapter 2), which revealed a level of population differentiation that is at the high end of the scale for forest trees. *P. macrocarpus* exhibited greater isozyme variability among populations (Chapter 2) than conifers (Yeh 1989; Boyle et al. 1991). This might be the result of reduced gene flow among populations because populations sampled in Thailand in this study are discontinuous. *P. macrocarpus* is an insect-pollinated species and the movement of pollinators might be confined among neighbouring trees within populations, although the recent studies of gene flow in tropical trees have demonstrated that pollen movement can be quite extensive at least on a scale of several hundred meters (Nason et al. 1996; Nason and Hamrick 1997). The limitation of gene flow among populations could therefore at least partially explain the significant differences among populations in growth and biomass traits observed in this study.

The family-within-population effect was generally large in relation to the population effect for all growth and biomass traits (Tables 4.10, 4.11 and 4.12). This result also conformed to that of isozyme analysis which also revealed approximately 87%

of total variability resided within population (Chapter 2). As pointed out by Yeh and Rasmussen (1985), sampling only the average and excellent phenotypes within stands could reduce the variability among the seed trees. In this study, seed trees were randomly sampled and there was no emphasis placed on the parental phenotypic superiority. Thus, this would contribute to maintaining the variability among seed trees.

Family variances were high and increased during seedling development. Although a decline in family variance was observed at older age, it remained relatively stable at 13% of the total variance toward the end of growing season (Table 4.10). High family variance observed at young age was probably due to growth under a competition-free environment which allowed better expression of the genetic potential (Bongarten and Hanover 1985; Wu et al. 1995). At older ages, the family variance diminished as intertree competition increased (Foster 1986).

Seed weight could also affect the patterns of family variance and genetic control over seedlings in this study. Seed weight as maternal or preconditioning effects has been demonstrated to influence seedling growth (e.g., Burgar 1964; Bonner 1988). Because seed weights of individual seedlings were also available, genetic correlations between seed weight and seedling growth traits were estimated (Table 4.22). It was obvious that seed weight affected seedling growth (Table 4.22). Genetic correlations between seed weight and height growth were high at young age and generally declined as the age advanced (from 0.727 at H3 to 0.377 at H30, Table 4.22) indicating the diminishing of maternal effect over seedling growth in *P. macrocarpus*. The decline in genetic correlations coincided with the decline in family variance over ages (Tables 4.10 and 4.22). On the other hand, genetic correlations between seed weight and diameter growth

were moderate and relatively stable over ages as observed in family variance (Tables 4.11 and 4.22). Similarly, moderate genetic correlations were also observed between seed weight and biomass traits (Table 4.22). Thus, the presence of maternal effects has an influence over the estimates of seedling genetic variance, heritability and genetic correlation, particularly for seedling height. It would be essential and beneficial to study the growth patterns of *P. macrocarpus* seedlings over several growth seasons in order to investigate the extent of maternal effect and age trends in the genetic control of growth, because knowledge of the genetic parameter trend over age will influence the efficiency of selection at an early age (Lambeth 1980; Lambeth et al. 1983; Gill 1987).

The narrow-sense heritabilities for individual (h_i^2) and family (h_f^2) varied among traits, from moderate to high (Table 4.14). Standard errors for those estimates were small relative to the size of the corresponding estimates indicating high precision for the estimates (Table 4.14). This was probably due to the uniform nursery environment and the efficient single-seedling plot design which exposed the family to the environment more evenly over the whole test and made replication more compact. In *P. macrocarpus* progeny-provenance trials currently established by ASEAN Forest Tree Seed Centre Project (AFTSC), Thailand, the estimates of individual heritability after one year of planting were relatively low (0.18 for height and 0.22 for diameter) (AFTSC, unpublished data) compared to the estimates in this study. Different degrees of environmental variation in the growth environment could have produced these differences in the estimates of heritability. Individual heritabilities of *P. macrocarpus* seedlings estimated in this study were also relatively high compared with most other forest trees (Cornelius 1994; Lokmal 1994; Wu et al. 1995; Paul et al. 1997).

In height growth, individual heritabilities (0.494 ± 0.078 to 1.00 ± 0.11) were more variable than family heritabilities (0.744 ± 0.036 to 0.895 ± 0.015) and also exhibited an age trend with heritability declining as age advanced (Table 4.14). The decline in individual heritabilities for height growth as seedling age advanced coincided with the decline in the family variances (Tables 4.10 and 4.14). Increased intertree competition as the trees grew diminished the family variance (Foster 1986) and would subsequently affect the decline in individual heritability estimates. As trees grow and intertree competition becomes more intense, the rate of height increment will decline (Namkoong and Conkle 1976). It has also been observed in this study that the rate of height growth decreased as seedling age advanced toward the end of the growth period (Table 4.6). This evidence would support the effect of intertree competition on genetic variance and heritability. Franklin (1979) also observed the decline in heritability of height growth as competition increased due to crown closure in the juvenile-genotypic phase. Other studies, however, reported different results in age trends of individual heritability for height growth. For instance, Cotterill and Dean (1988) reported an increase followed by a decrease in a thinned population of radiata pine. Bouvet and Vigneron (1995) observed an increase followed by a plateau in *Eucalyptus europhylla* x *E. Grandis* hybrids. Xie and Ying (1996) observed a decrease followed by an increase in lodgepole pine. It is, therefore, difficult to find a consistent pattern for changes in heritability for height. This may well illustrate the fact that genetic parameters should always be interpreted with caution because they are applicable only to the defined base population, reference selection unit, and reference test environment (Hanson 1963).

Seed weight as a maternal precondition would affect the changes in heritability estimates for height growth in *P. macrocarpus*. Genetic correlation between seed weight and height declined as seedling age advanced (Table 4.22). This implied that the maternal effect would inflate individual heritability estimates at a young age. However, it seemed that seed weight had less effect on the family heritability estimates, which were relatively stable over age, although a slight decrease was observed late in the growth period. As the potential influence of seed weight decreased with increasing seedling age, a more reliable estimate of heritability would be obtained.

Individual and family heritabilities for diameter growth were relatively stable among seedling ages (Table 4.14). The estimates were also high compared to other studies (e.g., Yeh and Heaman 1982; Otegbeye 1991; Wu et al. 1995). The seed weight effect also affected diameter growth and maintained a relatively high influence throughout the growth period (Table 4.22). This suggests that seed weight would have a prolonged effect on diameter growth compared with height growth.

A moderate level of genetic control was observed in biomass traits, except S:R and SLWT (Table 4.14). S:R exhibited high family heritability but low individual heritability (Table 4.14) which would be due to the large error variance among seedlings (Table 4.12). Individual seedlings in this study were genetically diverse because they were derived from open-pollinated families originating in diverse habitats. The genetic heterogeneity would result in variable growth and dry matter partitioning to shoot and to root among seedlings as reflected by large error variances (Table 4.12). Allocation of dry matter to shoot and to root was found to vary under different growth conditions (e.g., Gibson et al. 1995; Tan et al. 1995). SLWT exhibited low genetic control at individual

(0.094 ± 0.04) and family levels (0.324 ± 0.095) (Table 4.14). Leaf development is influenced by the growth conditions (Kitajima et al. 1997; Saelim 1997). Phenotypic plasticity of leaves under different growth conditions, such as light, water availability, etc., has been observed in many tree species (Abrams and Kubiske 1990; Abrams et al. 1994). Environmental influence on leaf structure and development would thus contribute to the low genetic control in SLWT in *P. macrocarpus*. Moderate genetic correlation between seed weight and biomass traits also indicated the presence of maternal effects as observed in height and diameter growth but the maternal effect appeared to be absent for S:R and SLWT (Table 4.22).

There were strong genetic correlations observed among the seedling traits studied in *P. macrocarpus*. Correlations for height growth involving younger seedling ages were generally lower than those observed between older seedling ages (Table 4.15). The higher correlations between later ages were probably due to maternal effects which diminished at older ages (Lambeth 1980). The genetic correlations between seed weight and height (Table 4.22), which also diminished at older seedling ages, would support this evidence. The genetic relationship between height and diameter was strong and stable over the seedling ages whereas higher genetic correlations between height and biomass traits were observed at older seedling ages (Table 4.16).

Seedling age-age correlations for diameter growth were also strong but did not exhibit any trends (Table 4.17). The absence of seedling age trends was also observed for the genetic correlations between diameter and biomass traits (Table 4.18). Except for S:R and SLWT, strong genetic correlations were also observed among the biomass traits, and related seedling parts generally exhibited higher estimates than the less related ones, i.e.,

LEAF had a higher genetic correlation with STEM than with TROOT (Table 4.19). It appeared that S:R and SLWT displayed moderate genetic correlation (0.462 ± 0.215) (Table 4.19). It is possible that the correlation observed between these two traits is spurious and is not indicative of a causative relationship. *P. macrocarpus* is a deciduous species and produces new leaves annually. Leaf morphology would vary from year to year depending on the growth conditions during leaf development (Kitajima et al. 1997; Saelim 1997). Thus, it is expected that correlation between SLWT and other traits would also vary.

Strong and positive genetic correlations observed for height, diameter and biomass traits suggested the potential to improve many traits simultaneously. Evaluation of families in nurserybeds would provide a preliminary screening for a large number of families at reasonable costs. Families with potentially superior performance would be selected and included in the subsequent progeny tests in the field. This would also reduce the cost in monitoring the trial. Furthermore, applying early selection to cull out the worst families, rather than to intensively select the very best (Mullin et al. 1995) would be of practical advantage for planting stock production in nursery operations.

4.4.2 Physiological traits

Net photosynthesis (*A*) in *P. macrocarpus* varied from 7.88 to 9.08 μmol m^{-2} s^{-1} among the six populations (Table 4.9). However, there were no significant differences in *A* among populations (Table 4.13). In this study, seedlings were grown under environmental conditions that most closely matched conditions at the origin of population 5; thus seedlings from population 5 exhibited the highest net photosynthesis. This result

suggests that the growth climate of seed origins could affect photosynthetic capacity in *P. macrocarpus*, in accordance with reports in other plants (Boltz et al. 1986; Cregg 1993; Cole et al. 1994; Gibson et al. 1995).

Transpiration (*E*) also varied among the populations and ranged from 1.31 to 1.49 mmol m^{-2} s^{-1} (Table 4.9). However, there were no significant differences in *E* among populations (Table 4.13). Seedlings from population 1 which has a slightly cooler climate exhibited the highest transpiration rate when they were grown under the warmer climate of population 5 (Tables 4.1 and 4.9). This would reflect the influence of climate of seed origins on transpiration as observed in *A*. Gibson et al. (1995) also observed higher transpiration in a hot growth cabinet than in a cool growth cabinet in *Eucalyptus camaldulensis* Dehnh. seedlings.

The relationship between *A* and *E* could be demonstrated in terms of water-use efficiency (WUE), which is defined as a rate of biomass accumulation expressed as carbon dioxide assimilation (*A*) to water consumed expressed as transpiration (*E*), i.e., WUE = *A*/*E* (Sinclair et al. 1984). Patterns of WUE among populations corresponded to that of *A* (Table 4.9). Seedlings from population 5 had the highest WUE as observed for *A* while seedlings from population 1 had the lowest WUE as a result of high *E* and low *A* (Table 4.9). Dunlap et al. (1993) also observed variation among seed sources in photosynthesis and water-use efficiency in *Populus triocarpa*. They found that clones from the xeric region generally had higher *A* and WUE than clones from the mesic region when they were grown under dry continental climate. The limitation of soil water supply (soil water deficits) results in a sequence of plant responses that involve reductions in growth (Pereira and Chaves 1993; Osório and Pereira 1994). In this study, seedlings were

grown in a container with limited soil volume. High transpiration rates would result in rapid depletion of water availability and subsequently water deficits. Low WUE of seedlings from population 1 associated with intermittent water deficits experienced during growth and development could result in their inferior growth and total biomass after the 30-week growth period compared with seedlings from population 5 which had the highest WUE (Tables 4.6, 4.7, 4.8 and 4.9).

Similar to height, diameter and biomass traits, genetic variation in physiological traits (*A*, *E* and WUE) was detected in *P. macrocarpus*. Population effect was highly significant only for WUE, while the family-within-population effect was highly significant for *A*, *E* and WUE (Table 4.13). The degree of variation as determined by percentage of total variance was comparable to that of the growth and biomass traits. Residual effects remained the largest proportion of variation (Table 4.13). Genetic variation in physiological traits or gas exchange was inconsistent among species. For instance, Larsen and Wellendorf (1990) found significant differences in *E* and WUE but not in *A* among 16 full-sib families of Norway spruce. Sulzer et al. (1993) did not detect significant differences in *A*, *E* and WUE among 20 half-sib black spruce families. Similarly, Dang et al. (1994) studied red alder (*Alnus rebra* Bong.) and did not find significant differences at the family level for photosynthesis, transpiration and water-use efficiency, but at the provenance level they observed significant differences for photosynthesis and transpiration but not for water-use efficiency. However, Zhang and Marshall (1994) reported the absence of significant differences in *A*, *E* and WUE among 14 populations of western larch. In this study, although *A* and *E* were not significantly different among populations, the significant difference in replication-by-population

interaction would suggest the existence of some degree of population differences in these two traits. Significant family effects for these three physiological parameters (*A*, *E* and WUE) also suggests that there is genetic differentiation in *A*, *E* and WUE in *P. macrocarpus*.

Moderate narrow-sense heritabilities suggest that *A*, *E* and WUE in *P. macrocarpus* seedlings are under genetic control (Table 4.14). Low standard errors also suggest high accuracy of the estimates. Generally, the heritability estimates for physiological traits were smaller than those for height and diameter growth but were comparable to some of the biomass traits (Table 4.14). Heritability estimates for gas exchange have rarely been documented in forest trees, although genetic variation in gas exchange has been well documented (e.g., Larsen and Wellendorf 1990; Sulzer et al. 1993; Dang et al. 1994). However, in some crop species, narrow-sense heritabilities for photosynthetic CO_2 uptake varied from 7% to 85% (Asay et al. 1974; Wallace et al. 1976; Crosbie et al. 1977; Harrison et al. 1981; Mahon and Hobbs 1981; Mahon 1983). Low heritabilities in *A*, *E* and WUE relative to height and diameter in this study implies strong environmental influence on these physiological parameters. Gas exchange has been reported to vary diurnally and seasonally (e.g., Boltz et al. 1986; Cole et al. 1994; Zine El Abidine et al. 1995). Doley et al. (1988) observed spatial and temporal distribution of photosynthesis and transpiration by single leaves in a rainforest tree, *Argyodendron peralatum*. Fredericksen et al. (1996) studied patterns of leaf gas exchange of different-sized *Prunus serotina* Ehrh. trees and observed that rates of gas exchange generally decreased with increasing tree size. They found that seedlings had higher leaf gas exchange rates than saplings, which had higher rates than canopy trees. Similarly,

Mebrahtu and Hanover (1991) observed that net photosynthetic rates declined with seedling age in black locust. Leaf phenotypes also affect photosynthetic characteristics (e.g., Kitajima et al. 1997). Despite environmental sensitivity, the moderate heritability estimates associated with low standard errors (Table 4.14) in this study indicate some degree of genetic control in *A*, *E* and WUE in *P. macrocarpus*. Significant genetic variation and moderate genetic control suggest the potential for genetic improvement of these physiological traits in *P. macrocarpus*.

Genetic correlations varied among physiological traits (Table 4.20). Photosynthesis had a high correlation with transpiration (0.782 ± 0.117) but was less correlated with water-use efficiency (0.104 ± 0.194). Transpiration, on the other hand, was negatively correlated with water-use efficiency (−0.481 ± 0.177). Dang et al. (1994) also observed significant and high phenotypic correlation between photosynthesis and transpiration (0.904) in red alder. However, a standard error for the estimate was not reported. It appears that this would be among the first studies where photosynthesis and transpiration were studied with a large number of families. High genetic correlation between these two physiological parameters associated with low standard error suggests that the estimate is reliable.

Photosynthesis, transpiration and water-use efficiency were not correlated or only weakly correlated with growth and biomass traits (Table 4.21). Mebrahtu and Hanover (1991) also observed weak correlations between net photosynthetic rate and different growth traits in black locust. Zhang et al. (1993) found no correlation between photosynthetic rate and height and diameter growth but observed strong correlation between water-use efficiency and height and diameter growth in Douglas-fir. The

inconsistent results or lack of correlations between physiological traits and growth and productivity could be due to several factors. These physiological traits were measured only on a few leaves for only a short period and may not be representative of final growth or productivity which is the net result of the integration of many processes over an extensive period. Physiological processes are also sensitive to environment (Mahon 1983; Meinzer et al. 1993; Major and Johnsen 1996). Dry matter production depends not only on the rate of photosynthesis per unit leaf area but also on total leaf area, leaf duration and canopy exposure (Kramer 1986). Because physiological processes are complicated and depend on limitations imposed by environment and plant structures (Mahon 1983), physiological processes, particularly photosynthesis, have met with limited success as predictors for future growth and productivity (e.g., Larsen and Wellendorf 1990; Sulzer et al. 1993). Greenwood and Volkaert (1992) also pointed out that a single measurement of photosynthetic rate or other physiological parameters is unlikely to give a generally applicable and reliable basis for early selection. In this study, the lack of correlations between physiological traits and growth and productivity suggests that physiolgical traits may not be useful parameters for early selection in *P. macrocarpus*, although they exhibited genetic variation and were under some degree of genetic control.

4.5 Conclusions

The existence of significant levels of genetic variation, genetic control and genetic relationship in growth, biomass and physiological traits suggests that there is potential and opportunity for the genetic improvement and early genetic selection in *P. macrocarpus*. The evaluation of seedling growth in this study, however, covered only one

growth season (six and a half months), which can hardly be sufficient for the profound knowledge of patterns of genetic variation, environmental influences and genetic parameters in *P. macrocarpus*. Nevertheless, this study provided a significant understanding and crucial information about patterns of genetic variation and genetic parameters of growth and physiological performance at early seedling ages. Testing *P. macrocarpus* in the field over more mature ages to complement nursery evaluation is crucial to understanding patterns of genetic inheritance in growth and physiological performance. Because *P. macrocarpus* covers a wide distribution range associated with a high level of population differentiation for forest trees (Chapter 2), it is also beneficial to include more test sites in the genetic test program in order to investigate the degree of genotype-by-environmental interaction. This knowledge is essential to guide establishment of breeding and deployment zones and to develop the proper strategies for genetic resources management and utilization in *P. macrocarpus*.

P. macrocarpus is a deciduous species and its leaf morphology may vary from year to year (Liengsiri, personal observation). Thus, assessment for one year may not be applicable to another. Representative measurements of physiological processes need to be developed so that the accuracy of parameter estimates could be determined. This would include assessment over several growth seasons and on several planting environments. Physiological measurement is tedious and complicated, and can be costly. This could limit the exploitation of physiological traits in genetic improvement. However, if physiological processes were to be incorporated in a genetic improvement program in *P. macrocarpus*, water-use efficiency would be a more promising trait than photosynthesis and transpiration. Testing and selecting of genotypes with high water-use efficiency

would be more important in reforestation program and for *ex situ* gene conservation where drought conditions are frequent and severe, such as on many degraded sites in Thailand. Deforestation in Thailand has caused severe soil erosion, reduction of soil fertility and water carrying capacity, and the adverse change in environment and site conditions which are required for seedling establishment and survival. As a consequence, reforestation on such degraded land seems troublesome. Although intensive site preparation and post-planting tending would improve the establishment and survival of seedlings, they can be very costly and are rarely practised in an operational reforestation in Thailand. Hence, the success of reforestation on such degraded sites must rely on the ability of seedlings to adapt and survive in such harsh conditions. High efficiency of water use is crucial not only for survival during seedling establishment (Cui and Smith 1991) but also for adapting to drier habitats (Monson and Grant 1989). Selecting genotypes or seed sources with the ability to maintain high water-use efficiency under water deficits is an initial step toward the success of reforestation and *ex situ* genetic conservation in *P. macrocarpus* on degraded land in Thailand.

In this study, there was an indication that families with low outcrossing rates were inferior to families with high outcrossing rates in their growth (Appendices 2 to 25). The presence of inbreeding in *P. macrocarpus* populations (Table 4.1) would suggest that the effect of inbreeding is also an important issue which needs to be incorporated in future genetic test programs of *P. macrocarpus*. Inbreeding depression has been well documented in forest trees (e.g., Eldridge and Griffin 1983; Hardner and Potts 1995; Williams and Savolainen 1996). Inbreeding also causes bias in genetic parameter estimates (Namkoong 1966; Squillace 1974).

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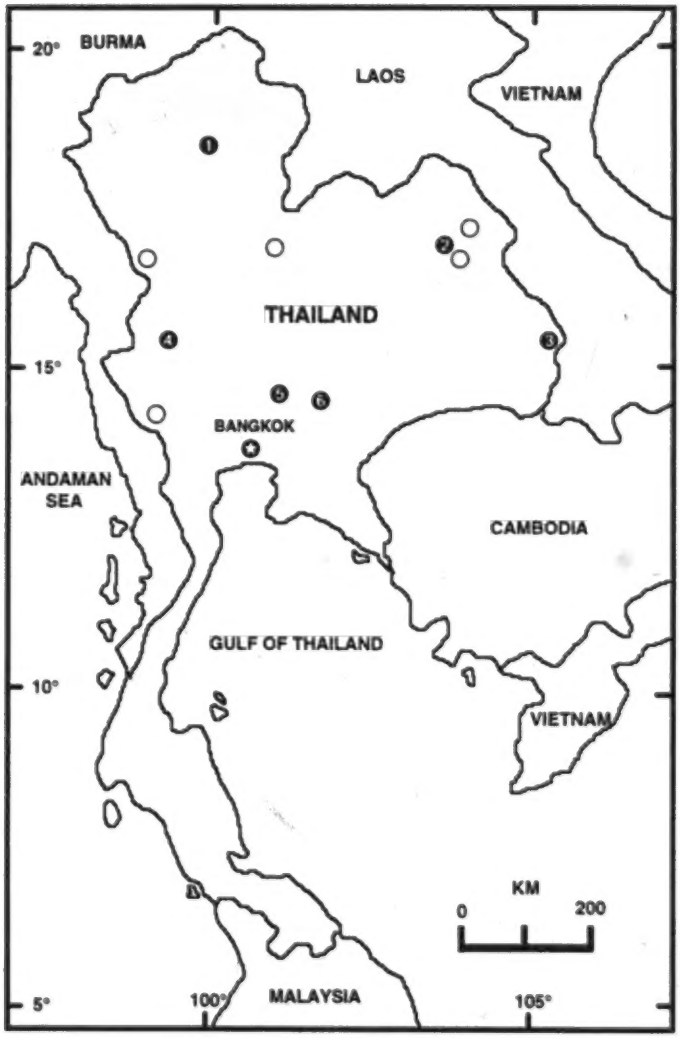

Figure 4.1 Map of Thailand showing locations of six populations of *P. macrocarpus* included in nursery study (●) and locations of other sampled populations (○).

Table 4.1 Geographic location, elevation, climatic information, forest type, inbreeding coefficient (F), multilocus outcrossing rate (t_m) and number of families of six populations of *P. macrocarpus* included in nursery trial.

Population		Latitude (°N)	Longitude (°E)	Elevation (m)	Mean annual temperature (°C)	Annual rainfall (mm)	Forest type [a]	F [b]	t_m [b]	No. of families
No.	Name									
1	Lampang	18°35'	99°54'	350	25.9 [c]	1076 [c]	MDF	-0.010	0.945	15
2	Phuphan-3	16°58'	103°45'	310	26.1 [c]	1587 [c]	DDF	0.144	0.751	14
3	Khong-chiam	15°24'	105°29'	200	26.7 [c]	1634 [c]	DDF	0.219	0.895	13
4	Uthaithani	15°30'	99°22'	220	N/A	N/A	DDF	0.090	0.953	21
5	Saraburi	14°35'	101°12'	200	26.1 [d]	1168 [d]	MDF	0.108	0.898	22
6	Sakaerat	14°25'	101°45'	380	26.3 [e]	1310 [e]	DDF	0.048	0.947	27

[a] MDF: mixed deciduous forest (moist site); DDF: dry dipterocarp forest (dry site).
[b] Estimates using isozyme data (see Chapter 3).
[c] Meteorological Department, Bangkok, Thailand (1961-1990).
[d] Thai-Danish Dairy Farm, Saraburi, Thailand (1976-1990).
[e] Sakaerat Environmental Research Station, Nakhonratchasima, Thailand (1980-1989).
N/A: data not available.

Table 4.2 Description of traits measured on *P. macrocarpus* seedlings grown in the nursery under ambient growth conditions in Thailand.

Abbreviation	Description
Height growth (cm)	
H3	Height at 3 weeks after sowing.
H6	Height at 6 weeks after sowing.
H9	Height at 9 weeks after sowing.
H12	Height at 12 weeks after sowing.
H15	Height at 15 weeks after sowing.
H18	Height at 18 weeks after sowing.
H21	Height at 21 weeks after sowing.
H24	Height at 24 weeks after sowing.
H27	Height at 27 weeks after sowing.
H30	Height at 30 weeks after sowing.
Diameter growth at root collar (mm)	
D12	Diameter at 12 weeks after sowing.
D15	Diameter at 15 weeks after sowing.
D18	Diameter at 18 weeks after sowing.
D21	Diameter at 21 weeks after sowing.
D24	Diameter at 24 weeks after sowing.
D27	Diameter at 27 weeks after sowing.
D30	Diameter at 30 weeks after sowing.
Biomass (dry weight) of plant part (g) assessed after 30-week growth period	
LEAF	Leaf dry weight.
STEM	Stem dry weight.
TROOT	Taproot dry weight.
FROOT	Fibrous root dry weight.
TOTAL	Total dry weight (i.e., LEAF + STEM + TROOT + FROOT).
SHOOT	Shoot portion dry weight (i.e., LEAF + STEM).
ROOT	Root portion dry weight (i.e., TROOT + FROOT).
S:R	SHOOT:ROOT ratio.
SLWT	Specific leaf weight (g m^{-2}); assessment of leaf dry weight (g) per unit leaf area (m^2). Four leaves were sampled and assessed for each seedling.
Physiological traits assessed during week-27 to week-29 of growth period	
A	Net photosynthesis (μmol m^{-2} s^{-1}).
E	Transpiration (mmol m^{-2} s^{-1}).
WUE	Water-use efficiency (μmol CO_2 /mmol H_2O); where WUE = *A*/*E*.

Table 4.3 Structure of analysis of variance and covariance for growth and biomass traits of *P. macrocarpus* seedlings grown in the nursery.

Source of variation	df	EMS or EMCP [a]
Replication	15	$\sigma_e^2 + k_1 \sigma_{f(p)}^2 + k_2 \sigma_{rp}^2 + k_3 \sigma_p^2 + k_4 \sigma_r^2$
Population	5	$\sigma_e^2 + k_5 \sigma_{f(p)}^2 + k_6 \sigma_{rp}^2 + k_7 \sigma_p^2$
Replication * Population	75	$\sigma_e^2 + k_8 \sigma_{f(p)}^2 + k_9 \sigma_{rp}^2$
Family (Population)	106	$\sigma_e^2 + k_{10} \sigma_{f(p)}^2$
Residual	1479	σ_e^2
Total	1680	

[a] EMS and EMCP are expected mean squares and expected mean cross-products, respectively.
σ_r^2, σ_p^2, σ_{rp}^2, $\sigma_{f(p)}^2$, and σ_e^2 are variances or covariances of replication, population, replication-by-population interaction, family within population, and residual, respectively.
$k_1 = 0.061$, $k_2 = 18.909$, $k_3 = 0.063$, $k_4 = 105.04$, $k_5 = 15.051$, $k_6 = 17.333$, $k_7 = 275.68$, $k_8 = 0.063$, $k_9 = 17.223$, $k_{10} = 14.953$.

Table 4.4 Structure of analysis of variance and covariance for physiological traits of *P. macrocarpus* seedlings grown in the nursery.

Source of variation	df	EMS or EMCP [a]
Replication	4	$\sigma_e^2 + k_1 \sigma_{l(fp)}^2 + k_2 \sigma_{f(p)}^2 + k_3 \sigma_{rp}^2 + k_4 \sigma_p^2 + k_5 \sigma_r^2$
Population	5	$\sigma_e^2 + k_6 \sigma_{l(fp)}^2 + k_7 \sigma_{f(p)}^2 + k_8 \sigma_{rp}^2 + k_9 \sigma_p^2$
Replication * Population	20	$\sigma_e^2 + k_{10} \sigma_{l(fp)}^2 + k_{11} \sigma_{f(p)}^2 + k_{12} \sigma_{rp}^2$
Family (Population)	106	$\sigma_e^2 + k_{13} \sigma_{l(fp)}^2 + k_{14} \sigma_{f(p)}^2$
Leaf (Family Population)	112	$\sigma_e^2 + k_{15} \sigma_{l(fp)}^2$
Residual	842	σ_e^2
Total	1089	

[a] EMS and EMCP are expected mean squares and expected mean cross-products, respectively.
σ_r^2, σ_p^2, σ_{rp}^2, $\sigma_{f(p)}^2$, $\sigma_{l(fp)}^2$ and σ_e^2 are variances or covariances of replication, population, replication-by-population interaction, family within population, leaf within family-within-population, and residual, respectively.
$k_1 = 0.027$, $k_2 = 0.049$, $k_3 = 39.224$, $k_4 = 0.049$, $k_5 = 218.0$, $k_6 = 4.876$, $k_7 = 9.746$, $k_8 = 35.793$, $k_9 = 178.78$, $k_{10} = 0.031$, $k_{11} = 0.055$, $k_{12} = 35.746$, $k_{13} = 4.863$, $k_{14} = 9.719$, $k_{15} = 4.862$.

Table 4.5 Percentage of seedling survival after the 30-week growth period.

Population	No. of families	Survival [a] (%)	Range among family survival (%)
1	15	95.83	75.00 - 100.00
2	14	97.32	93.75 - 100.00
3	13	93.75	75.00 - 100.00
4	21	92.26	75.00 - 100.00
5	22	94.60	75.00 - 100.00
6	27	96.53	87.50 - 100.00
Overall	112	95.03	75.00 - 100.00

[a] Averaged from family survival (%) after 30-week growth period.
There was no significant difference among populations for survival (%) after the 30-week growth period.

Table 4.6 Population means and standard deviations (SD), range of family means, grand means and coefficients of variation (C.V.) for height growth (cm) of *P. macrocarpus* seedlings grown in the nursery.

	Population							
	1	2	3	4	5	6		
Trait	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	Grand mean [a]	C.V. [b] (%)
H3	4.1 (0.81)	4.4 (0.98)	4.3 (0.85)	4.4 (0.84)	4.8 (0.78)	3.9 (0.76)	4.3	20.25
Range	3.2 - 4.9	3.6 - 5.5	3.5 - 5.1	3.7 - 5.4	4.0 - 5.5	3.0 - 5.1		
H6	6.8 (1.38)	7.0 (1.44)	7.0 (1.32)	7.3 (1.42)	7.7 (1.49)	6.4 (1.50)	7.0 (62.8%)	21.52
Range	6.1 - 8.0	5.2 - 8.3	5.7 - 8.8	6.1 - 9.1	6.4 - 9.7	5.0 - 7.5		
H9	10.2 (2.04)	11.7 (2.08)	11.7 (2.34)	11.4 (2.13)	13.1 (2.48)	11.0 (2.08)	11.6 (65.7%)	20.51
Range	8.4 - 11.4	9.5 - 13.5	8.9 - 14.7	9.8 - 14.2	10.3 - 15.7	8.1 - 13.0		
H12	16.5 (3.30)	18.9 (3.84)	18.6 (4.01)	19.1 (3.67)	21.9 (3.85)	18.1 (3.43)	19.0 (63.8%)	21.12
Range	14.0 - 19.4	15.0 - 22.6	14.5 - 23.6	16.5 - 23.1	17.5 - 26.5	14.9 - 22.5		
H15	19.2 (4.53)	22.4 (4.98)	22.2 (5.58)	23.3 (5.29)	25.1 (4.93)	21.4 (4.89)	22.4 (17.9%)	23.79
Range	16.5 - 23.1	18.4 - 27.2	18.9 - 29.9	20.5 - 29.6	19.9 - 30.6	17.3 - 25.1		
H18	24.8 (7.38)	28.0 (7.73)	29.1 (9.44)	30.8 (8.37)	31.9 (7.77)	27.8 (7.83)	28.9 (29.0%)	28.86
Range	19.9 - 31.1	23.0 - 33.7	24.0 - 37.7	24.7 - 38.8	26.4 - 39.9	20.5 - 32.9		
H21	27.8 (8.46)	29.6 (7.96)	32.5 (10.37)	34.2 (9.34)	35.9 (8.73)	31.2 (8.92)	32.2 (11.4%)	29.03
Range	23.3 - 35.2	23.8 - 35.5	26.6 - 41.7	28.7 - 41.9	28.2 - 46.5	22.7 - 36.6		
H24	28.6 (8.34)	30.2 (7.96)	33.7 (10.16)	35.3 (9.13)	37.2 (8.41)	32.2 (8.99)	33.2 (3.1%)	27.95
Range	24.9 - 35.5	23.9 - 36.0	27.9 - 42.3	29.1 - 45.2	30.2 - 47.3	24.2 - 39.0		
H27	29.3 (8.46)	31.1 (8.69)	34.6 (10.44)	36.4 (9.63)	40.0 (10.89)	35.4 (11.31)	35.0 (5.4%)	30.58
Range	25.1 - 35.7	24.3 - 37.9	28.4 - 43.2	29.5 - 46.1	31.2 - 50.9	25.4 - 44.5		
H30	29.8 (8.93)	31.7 (9.33)	35.5 (11.30)	37.2 (10.05)	40.9 (12.25)	37.2 (12.95)	36.2 (3.4%)	32.65
Range	26.1 - 35.8	24.4 - 38.4	28.7 - 45.8	29.5 - 47.3	31.9 - 51.9	25.8 - 47.5		

[a] Value in parentheses indicates percentage of growth increment from previous measurement.
[b] Coefficient of variation (%) based on individual observations.

Table 4.7 Population means and standard deviations (SD), range of family means, grand means and coefficients of variation (C.V.) for diameter growth (mm) of *P. macrocarpus* seedlings grown in the nursery.

	Population							
	1	2	3	4	5	6		
Trait	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	Grand mean [a]	C.V. [b] (%)
D12	3.13 (0.59)	3.40 (0.53)	3.30 (0.53)	3.30 (0.54)	3.48 (0.53)	3.25 (0.57)	3.31	16.87
Range	2.77 - 3.67	2.69 - 3.91	2.63 - 3.61	2.85 - 3.85	2.99 - 3.93	2.85 - 3.76		
D15	4.27 (0.82)	4.58 (0.82)	4.52 (0.82)	4.58 (0.87)	4.87 (0.75)	4.54 (0.81)	4.58 (38.4%)	18.08
Range	3.80 - 5.13	3.73 - 5.56	3.73 - 5.15	3.77 - 5.12	4.26 - 5.65	3.85 - 5.24		
D18	5.27 (0.98)	5.71 (1.08)	5.64 (1.07)	5.74 (1.07)	5.93 (1.00)	5.49 (0.95)	5.64 (23.1%)	18.38
Range	4.83 - 6.09	4.73 - 6.83	4.68 - 6.53	4.79 - 6.34	5.10 - 6.97	4.73 - 6.49		
D21	6.47 (1.21)	7.07 (1.47)	6.88 (1.49)	7.13 (1.37)	7.09 (1.24)	6.68 (1.11)	6.89 (22.2%)	19.10
Range	5.86 - 7.81	5.89 - 8.73	5.91 - 8.40	6.03 - 7.89	6.18 - 8.65	5.71 - 7.99		
D24	7.75 (1.46)	8.28 (1.63)	8.12 (1.60)	8.59 (1.62)	8.67 (1.54)	8.21 (1.44)	8.31 (20.6%)	18.81
Range	6.96 - 9.18	6.81 - 10.08	7.12 - 9.64	7.24 - 9.99	7.62 - 10.72	7.20 - 9.56		
D27	8.89 (1.69)	9.24 (1.91)	9.19 (1.83)	9.93 (1.95)	10.11 (1.86)	9.50 (1.73)	9.55 (14.9%)	19.62
Range	8.08 - 10.21	7.29 - 11.51	7.99 - 11.11	8.49 - 11.75	8.78 - 12.46	8.41 - 11.06		
D30	9.76 (1.89)	9.94 (2.01)	10.00 (2.01)	10.80 (2.16)	11.04 (1.91)	10.29 (1.85)	10.38 (8.7%)	19.42
Range	9.03 - 11.24	7.96 - 12.49	8.44 - 12.03	9.17 - 12.98	9.73 - 13.44	8.97 - 11.73		

[a] Value in parentheses indicates percentage of growth increment from previous measurement.
[b] Coefficient of variation (%) based on individual observations.

Table 4.8 Population means and standard deviations (SD), range of family means, grand means and coefficients of variation (C.V.) for biomass (g) of *P. macrocarpus* seedlings grown in the the nursery.

	Population							
	1	2	3	4	5	6		
Trait	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	Grand mean	C.V.[a] (%)
LEAF	2.077 (1.124)	2.306 (1.294)	2.662 (1.418)	3.188 (1.587)	4.048 (2.039)	3.164 (1.697)	3.027	57.23
Range	1.596 - 2.373	1.418 - 4.134	1.567 - 3.572	2.197 - 5.344	2.883 - 5.763	2.058 - 4.906		
STEM	2.364 (1.222)	2.750 (1.492)	2.923 (1.581)	3.815 (2.143)	4.124 (2.088)	3.051 (1.904)	3.254	59.17
Range	1.710 - 2.878	1.670 - 5.285	1.968 - 4.202	2.601 - 5.922	2.409 - 6.551	1.794 - 4.487		
TROOT	3.200 (1.874)	3.984 (2.190)	2.659 (1.712)	3.988 (2.303)	4.605 (2.310)	3.573 (1.839)	3.748	57.19
Range	1.675 - 4.131	2.243 - 6.230	1.145 - 3.845	2.423 - 6.107	2.904 - 7.187	2.243 - 4.826		
FROOT	1.124 (0.697)	1.275 (0.727)	1.341 (0.746)	1.310 (0.749)	1.657 (0.871)	1.324 (0.703)	1.356	56.82
Range	0.836 - 1.569	0.822 - 2.333	0.940 - 1.873	0.869 - 1.940	1.086 - 2.362	0.848 - 1.856		
TOTAL	8.741 (4.313)	10.309 (4.958)	9.571 (4.781)	12.292 (2.914)	14.429 (6.322)	11.108 (5.412)	11.375	50.50
Range	6.454 - 10.668	6.800 - 17.981	6.363 - 13.202	8.985 - 17.561	9.741 - 19.223	7.376 - 15.015		
SHOOT	4.441 (2.209)	5.056 (2.627)	5.585 (2.849)	7.003 (3.587)	8.172 (3.913)	6.215 (3.432)	6.281	55.52
Range	3.306 - 5.134	3.312 - 9.419	3.534 - 7.484	4.798 - 11.000	5.430 - 11.234	4.065 - 9.241		
ROOT	4.300 (2.402)	5.253 (2.651)	3.986 (2.238)	5.290 (2.837)	6.257 (2.912)	4.893 (2.333)	5.094	52.67
Range	2.458 - 5.666	3.293 - 8.562	2.158 - 5.718	3.423 - 7.634	4.018 - 8.954	3.311 - 6.681		
S:R	1.19 (0.57)	1.02 (0.36)	1.57 (0.70)	1.53 (0.78)	1.41 (0.60)	1.34 (0.54)	1.354	46.68
Range	0.87 - 1.89	0.87 - 1.23	1.17 - 2.11	0.99 - 2.23	1.12 - 1.92	1.07 - 1.79		
SLWT[b]	53.49 (9.52)	55.71 (8.63)	56.76 (9.72)	58.26 (8.70)	54.94 (8.17)	55.94 (9.19)	55.90	16.19
Range	49.61 - 60.45	51.48 - 62.70	50.94 - 60.30	54.65 - 63.31	48.99 - 60.67	51.18 - 62.37		

[a] Coefficient of variation (%) based on individual observations.
[b] Measurement unit: g m^{-2}.

Table 4.9 Population means and standard deviation (SD), range of family means, grand means and coefficients of variation (C.V.) for net photosynthesis (*A*), transpiration (*E*), and water-use efficiency (WUE) of *P. macrocarpus* seedlings grown in the nursery.

	Population							
	1	2	3	4	5	6		
Trait	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	Grand mean	C.V.[a] (%)
A[b]	7.98 (3.54)	7.93 (3.09)	7.88 (4.18)	8.54 (3.17)	9.08 (3.67)	8.40 (3.32)	8.39	41.69
Range	5.66 - 10.04	5.99 - 11.60	5.31 - 10.68	6.29 - 11.71	6.12 - 10.98	5.15 - 11.06		
E[c]	1.49 (0.76)	1.39 (0.65)	1.31 (0.73)	1.41 (0.62)	1.35 (0.63)	1.44 (0.74)	1.40	49.24
Range	1.13 - 2.18	1.09 - 1.96	0.89 - 1.86	0.99 - 2.03	0.98 - 1.90	0.91 - 2.48		
WUE[d]	5.82 (2.35)	6.26 (2.23)	6.45 (3.01)	6.58 (2.46)	7.28 (2.51)	6.54 (2.58)	6.56	39.07
Range	4.32 - 7.78	5.34 - 7.20	4.95 - 8.40	5.28 - 9.31	6.03 - 8.86	4.86 - 8.20		

[a] Coefficient of variation (%) based on individual observations.
[b] Measurement unit: $\mu mol\ m^{-2}\ s^{-1}$.
[c] Measurement unit: $mmol\ m^{-2}\ s^{-1}$.
[d] Measurement unit: $\mu mol\ CO_2/mmol\ H_2O$.

Table 4.10 Components of variance (percentage of total variance) and significant tests for height growth of *P. macrocarpus* seedlings grown in the nursery.

Source of variation	df	H3	H6	H9	H12	H15	H18	H21	H24	H27	H30
Replication	15	0.02 ns	0.18 ns	0.11 ns	1.19 **	4.57 **	7.72 **	10.60 **	9.45 **	10.02 **	9.89 **
Population	5	11.84 **	9.40 **	15.16 **	17.58 **	11.59 **	7.74 **	8.91 **	9.67 **	10.60 **	11.38 **
Replication * Population	75	0.00 ns	0.00 ns	0.00 ns	0.20 ns	0.00 ns	0.00 ns	0.00 ns	0.00 ns	0.13 ns	0.00 ns
Family (Population)	106	24.10 **	25.36 **	30.67 **	28.09 **	21.56 **	15.13 **	13.35 **	13.59 **	13.52 **	12.82 **
Residual	1479	64.04	65.05	54.06	52.94	62.29	69.42	67.14	67.29	65.73	65.90

ns: not significant; **: significant at $P < 0.01$.

Table 4.11 Components of variance (percentage of total variance) and significant tests for diameter growth of *P. macrocarpus* seedlings grown in the nursery.

Source of variation	df	D12	D15	D18	D21	D24	D27	D30
Replication	15	0.16 ns	0.00 ns	1.47 **	3.16 **	1.79 **	4.35 **	4.77 **
Population	5	2.72 *	3.27 **	3.34 **	2.57 *	2.61 *	4.28 **	4.67 **
Replication * Population	75	0.78 ns	0.55 ns	1.43 *	0.57 ns	0.58 ns	0.49 ns	0.03 ns
Family (Population)	106	18.08 **	19.36 **	18.62 **	21.02 **	18.00 **	16.46 **	17.03 **
Residual	1479	78.26	76.82	75.14	72.68	77.02	74.42	73.50

ns: not significant; *: significant at $P < 0.05$; **: significant at $P < 0.01$.

Table 4.12 Components of variance (percentage of total variance) and significant tests for biomass of *P. macrocarpus* seedlings grown in the nursery.

Source of variation	df	LEAF	STEM	TROOT	FROOT	TOTAL	SHOOT	ROOT	S:R	SLWT
Replication	15	7.79 **	10.12 **	6.14 **	4.49 **	9.49 **	9.79 **	6.44 **	1.20 **	12.88 **
Population	5	15.21 **	10.23 **	7.59 **	4.46 **	10.95 **	13.20 **	7.09 **	8.04 **	2.28 **
Replication * Population	75	0.18 ns	0.00 ns	0.08 ns	0.00 ns	0.21 ns	0.10 ns	0.00 ns	0.00 ns	0.64 ns
Family (Population)	106	10.33 **	14.83 **	13.29 **	11.59 **	13.66 **	12.86 **	13.26 **	8.72 **	2.62 **
Residual	1479	66.48	64.82	72.91	79.47	65.70	64.06	73.21	82.04	81.58

ns: not significant; **: significant at $P < 0.01$.

Table 4.13 Components of variance (percentage of total variance) and significant tests for physiological traits of *P. macrocarpus* seedlings grown in the nursery.[a]

Source of variation	df	*A*	*E*	WUE
Replication	4	0.27 ns	3.90 **	14.62 **
Population	5	0.00 ns	0.00 ns	2.34 **
Replication * Population	20	3.58 **	1.44 *	0.98 ns
Family (Population)	106	12.65 **	13.37 **	6.94 **
Leaf (Family Population)	112	0.00 ns	0.00 ns	0.00 ns
Residual	842	83.49	81.29	75.13

[a] Only 5 replications were assessed for physiological traits and two leaves from each seedling were measured.
ns: not significant; *: significant at $P < 0.05$; **: significant at $P < 0.01$.

Table 4.14 Estimates of individual (h_i^2) and family (h_f^2) heritabilities and their standard errors (s.e.) for height, diameter, biomass and physiological traits of *P. macrocarpus* seedlings grown in the nursery.

Trait	h_i^2	(s.e.)	h_f^2	(s.e.)
Height				
H3	0.829	(0.100)	0.849	(0.021)
H6	0.850	(0.101)	0.854	(0.021)
H9	1.000	(0.110)	0.895	(0.015)
H12	1.000	(0.109)	0.888	(0.016)
H15	0.779	(0.097)	0.838	(0.023)
H18	0.542	(0.082)	0.765	(0.033)
H21	0.503	(0.079)	0.748	(0.035)
H24	0.509	(0.079)	0.751	(0.035)
H27	0.517	(0.080)	0.755	(0.035)
H30	0.494	(0.078)	0.744	(0.036)
Diameter				
D12	0.569	(0.084)	0.776	(0.032)
D15	0.610	(0.087)	0.790	(0.030)
D18	0.602	(0.086)	0.787	(0.030)
D21	0.680	(0.092)	0.812	(0.026)
D24	0.574	(0.084)	0.777	(0.031)
D27	0.549	(0.083)	0.768	(0.033)
D30	0.570	(0.084)	0.776	(0.032)
Biomass				
LEAF	0.408	(0.071)	0.699	(0.042)
STEM	0.564	(0.084)	0.774	(0.032)
TROOT	0.467	(0.076)	0.732	(0.038)
FROOT	0.386	(0.069)	0.686	(0.044)
TOTAL	0.522	(0.080)	0.757	(0.034)
SHOOT	0.507	(0.079)	0.750	(0.035)
ROOT	0.465	(0.076)	0.730	(0.038)
S:R	0.291	(0.060)	0.614	(0.054)
SLWT	0.094	(0.040)	0.324	(0.095)
Physiological trait				
A	0.399	(0.090)	0.596	(0.077)
E	0.428	(0.092)	0.615	(0.073)
WUE	0.256	(0.079)	0.473	(0.100)

Table 4.15 Estimates of genetic correlations (above diagonal) and their standard errors (below diagonal) among height growth of *P. macrocarpus* seedlings grown in the nursery.

	H3	H6	H9	H12	H15	H18	H21	H24	H27	H30
H3	*****	0.655	0.658	0.721	0.672	0.551	0.520	0.502	0.422	0.394
H6	0.066	*****	0.875	0.814	0.791	0.698	0.700	0.690	0.635	0.598
H9	0.065	0.030	*****	0.956	0.915	0.811	0.798	0.793	0.691	0.655
H12	0.058	0.042	0.014	*****	0.960	0.858	0.847	0.834	0.733	0.699
H15	0.068	0.050	0.025	0.012	*****	0.953	0.922	0.909	0.824	0.787
H18	0.089	0.070	0.049	0.038	0.019	*****	0.979	0.963	0.921	0.892
H21	0.094	0.072	0.053	0.042	0.028	0.011	*****	0.997	0.977	0.963
H24	0.095	0.072	0.053	0.044	0.030	0.014	0.001	*****	0.989	0.978
H27	0.102	0.079	0.068	0.060	0.045	0.025	0.009	0.006	*****	0.997
H30	0.105	0.084	0.073	0.066	0.053	0.032	0.015	0.011	0.003	*****

Table 4.16 Estimates of genetic correlations (r_g) and their standard errors (s.e.) between height and diameter and biomass traits of *P. macrocarpus* seedlings grown in the nursery.

r_g	H3	H6	H9	H12	H15	H18	H21	H24	H27	H30
D12	0.546	0.593	0.796	0.785	0.732	0.618	0.637	0.646	0.580	0.563
s.e	0.089	0.083	0.051	0.050	0.060	0.082	0.083	0.081	0.089	0.092
D15	0.648	0.680	0.857	0.887	0.863	0.766	0.761	0.764	0.699	0.685
s.e	0.076	0.072	0.042	0.035	0.041	0.060	0.063	0.062	0.072	0.075
D18	0.682	0.722	0.873	0.917	0.882	0.749	0.733	0.738	0.664	0.641
s.e	0.072	0.067	0.041	0.032	0.039	0.064	0.066	0.065	0.076	0.081
D21	0.619	0.719	0.811	0.865	0.870	0.762	0.725	0.727	0.647	0.621
s.e	0.078	0.066	0.048	0.039	0.039	0.061	0.068	0.067	0.078	0.082
D24	0.595	0.695	0.821	0.872	0.875	0.780	0.738	0.746	0.675	0.658
s.e	0.084	0.071	0.049	0.040	0.041	0.059	0.067	0.066	0.075	0.079
D27	0.574	0.702	0.817	0.865	0.876	0.805	0.775	0.784	0.721	0.698
s.e	0.087	0.071	0.050	0.042	0.041	0.055	0.060	0.058	0.068	0.072
D30	0.609	0.740	0.829	0.872	0.874	0.797	0.765	0.770	0.699	0.676
s.e	0.082	0.065	0.048	0.040	0.040	0.056	0.061	0.059	0.070	0.074
LEAF	0.297	0.577	0.527	0.547	0.660	0.754	0.779	0.787	0.817	0.805
s.e	0.116	0.092	0.094	0.091	0.078	0.066	0.061	0.059	0.049	0.050
STEM	0.542	0.740	0.793	0.816	0.879	0.892	0.879	0.882	0.859	0.843
s.e	0.089	0.064	0.052	0.046	0.035	0.034	0.035	0.034	0.037	0.041
TROOT	0.504	0.502	0.529	0.569	0.669	0.730	0.626	0.588	0.583	0.556
s.e	0.096	0.096	0.091	0.085	0.074	0.067	0.083	0.088	0.089	0.094
FROOT	0.401	0.561	0.629	0.694	0.779	0.812	0.803	0.787	0.753	0.743
s.e	0.110	0.095	0.084	0.075	0.064	0.059	0.061	0.063	0.067	0.070
TOTAL	0.503	0.665	0.689	0.725	0.823	0.879	0.842	0.829	0.823	0.803
s.e	0.094	0.076	0.069	0.062	0.047	0.037	0.044	0.045	0.045	0.049
SHOOT	0.454	0.695	0.705	0.727	0.815	0.864	0.868	0.873	0.873	0.858
s.e	0.100	0.072	0.067	0.062	0.049	0.041	0.039	0.037	0.034	0.037
ROOT	0.512	0.553	0.593	0.643	0.745	0.803	0.718	0.683	0.669	0.645
s.e	0.096	0.091	0.083	0.076	0.063	0.054	0.069	0.074	0.076	0.081
S:R	-0.116	0.207	0.156	0.115	0.079	0.069	0.216	0.263	0.306	0.318
s.e	0.132	0.129	0.128	0.129	0.134	0.140	0.138	0.136	0.132	0.131
SLWT	-0.137	0.074	0.173	0.176	0.215	0.107	0.113	0.095	0.044	0.045
s.e	0.183	0.183	0.177	0.177	0.179	0.192	0.193	0.193	0.195	0.196

Table 4.17 Estimates of genetic correlations (above diagonal) and their standard errors (below diagonal) among diameter growth of *P. macrocarpus* seedlings grown in the nursery.

	D12	D15	D18	D21	D24	D27	D30
D12	*****	0.972	0.911	0.878	0.890	0.870	0.857
D15	0.019	*****	0.990	0.968	0.961	0.945	0.908
D18	0.033	0.011	*****	0.984	0.977	0.976	0.950
D21	0.039	0.019	0.011	*****	1.000	0.988	0.971
D24	0.040	0.022	0.016	0.006	*****	0.992	0.973
D27	0.045	0.026	0.018	0.010	0.006	*****	0.996
D30	0.046	0.032	0.022	0.014	0.011	0.004	*****

Table 4.18 Estimates of genetic correlations (r_g) and their standard errors (s.e.) between diameter and biomass traits of *P. macrocarpus* seedlings grown in the nursery.

r_g	D12	D15	D18	D21	D24	D27	D30
LEAF	0.485	0.616	0.567	0.577	0.561	0.603	0.585
s.e	0.104	0.087	0.093	0.089	0.092	0.086	0.087
STEM	0.725	0.844	0.847	0.849	0.853	0.892	0.879
s.e	0.067	0.045	0.044	0.041	0.041	0.032	0.034
TROOT	0.436	0.667	0.608	0.586	0.541	0.543	0.507
s.e	0.106	0.077	0.085	0.087	0.094	0.093	0.097
FROOT	0.624	0.768	0.714	0.743	0.737	0.727	0.717
s.e	0.090	0.067	0.074	0.069	0.070	0.070	0.072
TOTAL	0.619	0.798	0.758	0.756	0.736	0.761	0.737
s.e	0.083	0.054	0.060	0.059	0.062	0.057	0.060
SHOOT	0.646	0.775	0.755	0.760	0.756	0.797	0.782
s.e	0.080	0.059	0.061	0.058	0.059	0.050	0.052
ROOT	0.517	0.741	0.679	0.670	0.631	0.631	0.599
s.e	0.097	0.066	0.075	0.075	0.082	0.081	0.085
S:R	0.195	0.071	0.125	0.151	0.210	0.268	0.283
s.e	0.137	0.138	0.137	0.134	0.135	0.133	0.131
SLWT	0.227	0.096	0.008	0.129	0.182	0.083	0.086
s.e	0.189	0.190	0.192	0.185	0.187	0.192	0.191

Table 4.19 Estimates of genetic correlations (above diagonal) and their standard errors (below diagonal) among biomass traits of *P. macrocarpus* seedlings grown in the nursery.

	LEAF	STEM	TROOT	FROOT	TOTAL	SHOOT	ROOT	S:R	SLWT
LEAF	*****	0.852	0.670	0.815	0.908	0.951	0.756	0.295	-0.088
STEM	0.039	*****	0.709	0.874	0.943	0.972	0.803	0.239	0.015
TROOT	0.078	0.067	*****	0.663	0.874	0.719	0.980	-0.403	-0.306
FROOT	0.055	0.042	0.079	*****	0.888	0.881	0.800	0.032	0.036
TOTAL	0.025	0.016	0.032	0.034	*****	0.964	0.939	0.018	-0.126
SHOOT	0.014	0.008	0.066	0.040	0.010	*****	0.813	0.273	-0.031
ROOT	0.062	0.050	0.006	0.051	0.017	0.048	*****	-0.314	-0.236
S:R	0.137	0.133	0.120	0.150	0.142	0.133	0.128	*****	0.462
SLWT	0.205	0.193	0.201	0.205	0.199	0.198	0.203	0.215	*****

Table 4.20 Estimates of genetic correlations and their standard errors (in parentheses) among physiological traits of *P. macrocarpus* seedlings grown in the nursery.

	A	*E*	WUE
A	*****	0.782 (0.117)	0.104 (0.194)
E		*****	-0.481 (0.177)
WUE			*****

Table 4.21 Estimates of genetic correlations (r_g) and their standard errors (in parentheses) between physiological traits and growth and biomass traits of *P. macrocarpus* seedlings grown in the nursery.[a]

r_g	*A*	*E*	WUE
H3	0.070 (0.139)	-0.023 (0.137)	0.158 (0.155)
H6	0.048 (0.140)	-0.054 (0.137)	0.149 (0.155)
H9	-0.018 (0.135)	-0.108 (0.132)	0.194 (0.149)
H12	0.038 (0.135)	-0.048 (0.133)	0.167 (0.150)
H15	0.061 (0.143)	-0.070 (0.139)	0.194 (0.158)
H18	0.057 (0.147)	-0.015 (0.144)	0.092 (0.165)
H21	0.067 (0.147)	-0.082 (0.144)	0.240 (0.162)
H24	0.096 (0.147)	-0.064 (0.144)	0.261 (0.161)
H27	0.086 (0.147)	-0.119 (0.143)	0.310 (0.160)
H30	0.070 (0.149)	-0.148 (0.145)	0.323 (0.162)
D12	-0.050 (0.144)	-0.127 (0.140)	0.127 (0.161)
D15	-0.076 (0.145)	-0.157 (0.140)	0.135 (0.162)
D18	-0.028 (0.146)	-0.086 (0.142)	0.088 (0.163)
D21	-0.008 (0.140)	-0.096 (0.137)	0.037 (0.157)
D24	-0.023 (0.142)	-0.090 (0.138)	0.069 (0.159)
D27	-0.035 (0.144)	-0.139 (0.140)	0.107 (0.161)
D30	-0.019 (0.143)	-0.136 (0.139)	0.144 (0.159)
LEAF	-0.173 (0.149)	-0.322 (0.140)	0.272 (0.166)
STEM	0.008 (0.145)	-0.138 (0.140)	0.218 (0.160)
TROOT	0.005 (0.148)	-0.130 (0.143)	0.195 (0.164)
FROOT	-0.084 (0.151)	-0.143 (0.146)	0.029 (0.170)
TOTAL	-0.056 (0.148)	-0.216 (0.141)	0.242 (0.163)
SHOOT	-0.073 (0.147)	-0.230 (0.140)	0.256 (0.161)
ROOT	-0.020 (0.148)	-0.147 (0.143)	0.165 (0.165)
S:R	-0.132 (0.146)	-0.188 (0.141)	0.124 (0.164)
SLWT	0.136 (0.154)	0.059 (0.151)	0.058 (0.175)

[a] Only five replications were included in the analysis.

Table 4.22 Genetic correlations (r_g) and standard errors (in parentheses) between seed weight (SWT) and other traits.

r_g	SWT	r_g	SWT
H3	0.727 (0.055)	LEAF	0.469 (0.096)
H6	0.656 (0.064)	STEM	0.584 (0.078)
H9	0.639 (0.064)	TROOT	0.579 (0.082)
H12	0.677 (0.059)	FROOT	0.550 (0.090)
H15	0.641 (0.067)	TOTAL	0.609 (0.077)
H18	0.491 (0.089)	SHOOT	0.555 (0.083)
H21	0.481 (0.091)	ROOT	0.611 (0.079)
H24	0.468 (0.092)	S:R	-0.079 (0.125)
H27	0.411 (0.097)	SLWT	0.064 (0.172)
H30	0.377 (0.100)		
D12	0.630 (0.073)	*A*	0.057 (0.129)
D15	0.731 (0.058)	*E*	-0.043 (0.127)
D18	0.772 (0.052)	WUE	0.191 (0.142)
D21	0.684 (0.063)		
D24	0.624 (0.073)		
D27	0.624 (0.074)		
D30	0.635 (0.072)		

CHAPTER 5

GAS EXCHANGE AND WATER RELATIONS IN RESPONSE TO WATER STRESS IN *PTEROCARPUS MACROCARPUS* SEEDLINGS

5.1 Introduction

Water availability is one of the most important factors affecting plant growth and development (Kramer 1983). Water stress affects a wide variety of physiological processes in plants because many important physiological processes, such as leaf enlargement, stomatal opening and photosynthesis, are directly affected by a reduction in leaf water potential (Hanson and Hitz 1982). The ability of plants to survive and grow under water stress also varies among species (e.g., Ranney et al. 1990; Ni and Pallardy 1991; Reekie and Wayne 1992; Lemcoff et al. 1994) and among genotypes within species (e.g., Abrams et al. 1990; Gebre and Kuhns 1993; Tan et al. 1995; Tognetti et al. 1995).

Plants adapt to or resist drought conditions using a variety of adaptive characteristics and mechanisms of morphological or physiological changes. Reekie and Wayne (1992) observed changes in leaf angle and leaf canopy display in seedlings of some tropical pioneer tree species when subjected to drought. Abrams (1988) found leaves of eastern redbud (*Cercis canadensis* L.) from xeric sites display the characteristics of sun leaves which are smaller, thicker and have more dense stomata compared with leaves of plants from more mesic areas. Tan et al. (1995) did not observe differences among black spruce (*Picea mariana* [Mill.] B.S.P.) families in root dry weight allocation of seedlings under well-watered condition, but under water stress condition seedlings from drought sensitive families allocated more dry weight to their roots at the expense of

shoot growth in order to postpone the onset of drought symptoms. Leaf abscission is also an important mechanism of reducing water loss to avoid the development of extreme water stress (Kozlowski 1976).

A number of studies have also documented physiological adaptations to water stress in plant species. Modification of stomatal behaviour and function appears to be a crucial mechanism in drought resistance (Kramer 1983). Under water stress, photosynthesis, stomatal conductance and transpiration normally decrease as a result of stomatal closure (e.g., Abrams et al. 1990; Tognetti et al. 1995). Stomatal closure is an effective mechanism to prevent water loss and maintain high plant water status under drought conditions (Zine El Abidine et al. 1994; Tognetti et al. 1995). Ranney et al. (1990) and Ni and Pallardy (1991) found that several plant species increase efficiency of water use under drought conditions to maintain positive plant water status. Several plant species also maintain physiological functions at low water potential through tissue osmotic adjustment (e.g., Gebre and Kuhns 1993; Edwards and Dixon 1995) and tissue elasticity (e.g., Abrams et al. 1990; Ranney et al. 1990). Lemcoff et al. (1994) found different magnitudes in osmotic adjustment among several *Eucalyptus* species under drought stress and suggested to use this plant feature as a selection criterion for genotypes that are adapted to drought-prone environments. Modification of stomatal conductance by water stress preconditioning was also reported for several *Populus* clones (e.g., Schulte et al. 1987; Gebre and Kuhns 1993). Zine El Abidine et al. (1994) also found that preconditioned seedlings maintained significantly higher net photosynthetic rate, stomatal conductance, and transpiration rate than unconditioned seedlings.

Pterocarpus macrocarpus Kurz is a deciduous tropical forest tree species indigenous to Thailand, Burma, Laos, Cambodia and extends to southern Vietnam (Rojo 1977). The wide range of its natural distribution and habitats may condition in its evolution and physiological adaptations to a particular habitat. Isozyme analysis (Chapter 2) and morphological and physiological studies (Chapter 4) have revealed a high level of genetic variation among populations of *P. macrocarpus* sampled from Thailand. However, knowledge pertaining to physiological responses to adverse environments, such as drought, among different ecotypes seem obscure despite its ecological and economical importance. Physiological differentiation among populations along environmental gradients has been reported for several tree species (e.g., Ledig and Koroboro 1983; Abrams 1988; Abrams et al. 1990). Many species are also capable of physiological plasticity in response to varying environmental conditions (e.g., Ranney et al. 1990; Ni and Pallardy 1991; Lemcoff et al. 1994). The objectives of this study were (1) to investigate the pattern of gas exchange and water relations in response to water stress of *P. macrocarpus* seedlings from different populations from Thailand and (2) to determine the magnitude of water stress tolerance of *P. macrocarpus* seedlings.

5.2 Materials and methods

5.2.1 Plant materials

Open-pollinated seeds of *P. macrocarpus* collected from Thailand were used in this study. A total of 18 families from three populations (Figure 5.1) representing different forest habitats was included in the study. These 18 families were a subset of 287 families from 11 populations used for the isozyme variation study (Chapter 2) and were

also included in morphological and physiological variation studies (Chapter 4). Details of geographic locations, climate, forest type, and number of sampled trees are presented in Table 5.1. Selection of six families within each of three populations was based on 12-week height growth information obtained from the study in Chapter 4. These six families within each population constituted two families from each of three growth-rate classes, that is, slow, medium and fast. This was done to include different growth performance among seedlings within populations.

Two hundred and forty seeds from each of 18 families were sampled for the study. Seeds were scarified individually with medium grain sand paper in order to eliminate seedcoat dormancy and to enhance rapid and uniform germination (Liengsiri 1987). A 24-cell multipot tray was used for seed germination and early seedling growth. The size of each cell was 2 inches in diameter and 4 inches in depth with an approximate volume of 190 ml. A single seed was sown into each cell. The planting medium was a mixture of coconut husk fibre, sand and compost in a 2:1:1 ratio with pH 7.5. Multipot trays were arranged by family for ease of operation. Seeds were sown in mid January 1995. Germination was completed within 10 days after sowing. Approximately 0.5 g of 2-month formula controlled release fertilizer (Osmocote 13-13-13) was supplied for each seedling 3 weeks after sowing. Seedlings were raised for 7 weeks before being transplanted into larger pots.

Approximately 100-120 healthy seedlings from each of 18 families were randomly selected and transplanted into 3-liter volume clay pots (7-inch diameter and 8-inch depth) filled with the same mixture of planting medium used for germination and early growth. Within each pot, two seedlings from the same family with similar size

(height) were grown together. This was done to minimize possible variation in soil moisture between the two seedlings at time of water stress assessment. Spacing between the two seedlings within the same pot was approximately 4 inches. Seedlings were allowed to grow and recover from transplanting shock. Water was daily supplied to maintain adequate soil moisture. Nursery conditions during seed germination and seedling growth were 24°C, 70% R.H. and 680 μmol m^{-2} s^{-1} photosynthetic active radiation (PAR).

At week 11, seedlings were rearranged for water stress assessment. One pot from each of 18 families was randomly sampled and arranged into groups. Each group therefore comprised 18 pots from which each pot represented each of 18 families. The arrangement of pots within each 18-pot group was random. Because two water stress cycles were planned for the study, therefore these 18-pot groups were equally divided into two sets and each set was used for each water stress cycle. Within each set, they were further equally divided into two subsets, one for well-watered (control) treatment and the other for water-stressed (stress) treatment. No randomization between pre-arranged control and stress seedlings was made in order to prevent any possible mistake in irrigation during water stress treatment. The water stress experiment was commenced when seedlings were 12 weeks old. The average height of seedlings at 12 weeks old was 15.4 cm.

5.2.2 Water stress treatment

Two water stress cycles were designed. The first cycle of water stress (cycle-1) was started on April 12, 1995 and completed on April 29, 1995 (Table 5.2). At the start of

the water stress cycle (Day 0), all seedlings were well watered. Water was thereafter withheld from seedlings subjected to water stress treatment while water was daily supplied to control seedlings. Water stress was continued for a 10-day period. After the completion of the 10-day water stress cycle, the stress seedlings were re-watered and allowed to recover for 7 days with daily watering.

In the second water stress cycle (cycle-2), seedlings were exposed to a 7-day period of water stress preconditioning. The preconditioning was started on April 12, 1995 (the same day on which cycle-1 started) and was terminated on April 19, 1995. At the beginning of the preconditioning, seedlings were well watered. Water was thereafter withheld from stress seedlings but was regularly supplied to control seedlings. No measurement was carried out during the preconditioning. After a 7-day period of water stress preconditioning, only 4% of the preconditioned seedlings remained turgid while the other 96% had wilted. However, no leaf injury was observed. To avoid irreversible leaf injury, all preconditioned seedlings were rewatered. On the next day following rewatering, all preconditioned seedlings recovered from wilting. Watering was continued for 7 days to allow preconditioned seedlings to fully recover from water stress prior to the beginning of the second water stress cycle.

The second cycle of water stress (cycle-2) was commenced on April 26, 1995 and was completed on May 17, 1995 (Table 5.2). All seedlings were well watered at the beginning of the water stress treatment (Day 0). Water was thereafter withheld from stress seedlings but was daily supplied to control seedlings. The water stress treatment for cycle-2 was continued for 14 days. After the completion of the 14-day water stress

treatment, the stress seedlings were rewatered and allowed to recover for 7 days with daily watering.

5.2.3 Data collection

Data collection was carried out in a similar manner in both cycle-1 and cycle-2. Measurements in response to water stress included gas exchange and water relations (details below). In cycle-1, data collection was carried out every second day from Day 0 to Day 6. Thereafter, daily data collection was made until the end of the 10-day water stress cycle (Table 5.2). Data collection was also conducted after 7 days of water stress recovery (Day 17).

In cycle-2, data collection was made on every second day during the 14-day water stress treatment and after 7 days of recovery. Details of sampling date and its corresponding day of the stress cycle are also given in Table 5.2.

On each day of data collection, 18 pots which were previously arranged in a group were sampled from both control and stress treatments. Two seedlings of the same family planted in the same pot were both sampled. A total of 36 seedlings were sampled for each treatment (control and stress) for the measurements of gas exchange and water relations.

To follow the progress of water stress development, soil moisture content was determined on each sampling day. Approximately 50 ml of soil were taken from the center of each pot. Eighteen soil samples were obtained and determined for moisture content for control and stress. Soil samples were weighed, oven-dried at 105°C for 24 hours and then reweighed. Soil moisture content was expressed as percentage of the oven-dry weight of the soil (Table 5.2).

5.2.3.1 Gas exchange

Measurements of gas exchange included net photosynthesis, transpiration and water-use efficiency. Net photosynthesis (*A*) and transpiration (*E*) were simultaneously measured using portable infrared gas analyzer (IRGA) (CI-301 Photosynthesis System, CID, Inc., USA). Water-use efficiency (WUE) was determined from *A* and *E*, where WUE = *A*/*E* (Sinclair et al. 1984). One mature and fully expanded leaf from each seedling was randomly assigned for measurements. Measurements were carried out under full sunlight during 8:00-11:30 hour. The average PAR during the measurements was 1,200 μmol m^{-2} s^{-1}. Although photosynthesis at light saturation of *P. macrocarpus* has not yet been reported, light intensity (PAR) was considered adequate to obtain maximum photosynthetic rate (Limpiyaprapant 1993). Each measurement was conducted for 30 seconds inside a 1-liter closed system CID leaf chamber. Alternative measurements were made between control and stress treatments. Sampling of pots within the treatment was random.

5.2.3.2 Water relations

Xylem water potential (Ψ_X) was determined by using a pressure chamber (Model 600, PMS Instruments Co., Corvallis, Oregon, USA) after the gas exchange measurements. A young stem was severed approximately 5 inches from the shoot tip. Fresh bark was gently peeled off to expose approximately 1.0 cm xylem at the cut end. The whole shoot was then used for the measurement.

5.2.4 Data analysis

Analysis of variance was performed for *A*, *E*, WUE and Ψ_X using the following general linear model:

$$Y_{ijkl} = \mu + T_i + P_j + TP_{ij} + F_k(P_j) + TF_{ik}(P_j) + E_{ijkl}$$

where

μ - grand mean

T_i - i^{th} treatment effect, i = 1-2

P_j - j^{th} population effect, j = 1-3

TP_{ij} - effect of treatment by population interaction

$F_k(P_j)$ - k^{th} family effect within the j^{th} population, k = 1-6

$TF_{ik}(P_j)$ - effect of treatment by family-within-population interaction

E_{ijkl} - residual error

SAS statistical package (SAS Institute Inc., Cary, NC) was employed for the analysis. Because only a few populations and families within population were included in the experiment, all effects in the model were considered to be fixed. The analysis of variance was performed for data collected on each sampling day throughout the course of water stress experiment.

5.3 Results

5.3.1 Net photosynthesis

Net photosynthesis (*A*) of seedlings grown under well-watered (control) conditions was generally higher than that of seedlings grown under water-stressed (stress) conditions in both cycle-1 and cycle-2 (Tables 5.3 and 5.5; Figures 5.2A and 5.2B). In

cycle-1, *A* of control seedlings ranged from 8.53 μmol m^{-2} s^{-1} on Day 8 to 12.78 μmol m^{-2} s^{-1} on Day 17 whereas *A* of stress seedlings declined from 9.73 μmol m^{-2} s^{-1} on Day 0 to 1.49 μmol m^{-2} s^{-1} on Day 10 as water stress developed (Table 5.3; Figure 5.2A). *A* of stress seedlings was significantly lower than that of control seedlings during the water stress treatment (Table 5.4; Figure 5.2A). However, stress seedlings recovered after rewatering and achieved a value of *A* (10.88 μmol m^{-2} s^{-1}) that was slightly lower than that of control seedlings (12.78 μmol m^{-2} s^{-1}) on Day 17 (Table 5.3; Figure 5.2A).

In cycle-2, *A* of control seedlings ranged from 9.36 μmol m^{-2} s^{-1} on Day 6 to 12.78 μmol m^{-2} s^{-1} on Day 0 (Table 5.5). *A* of stress seedlings was similar to *A* of control seedlings during the early period of water stress treatment (Day 0 to Day 6) (Tables 5.5 and 5.6; Figure 5.2B). However, *A* of stress seedlings declined and was significantly lower than *A* of control seedlings after 6 days of water stress treatment (Tables 5.5 and 5.6; Figure 5.2B). After 14 days of water stress, *A* of stress seedlings decreased to less than 1.0 μmol m^{-2} s^{-1} (0.94 μmol m^{-2} s^{-1} on Day 14; Table 5.5), but it recovered when stress seedlings were rewatered. On Day 21 (7-day recovery after 14-day water stress) *A* of control and stress seedlings were similar, 11.44 and 10.64 μmol m^{-2} s^{-1}, respectively (Tables 5.5 and 5.6).

There were significant differences in *A* among populations observed on Days 0 and 10 in cycle-1 (Table 5.4) and on Days 4, 8 and 12 in cycle-2 (Table 5.6) during the water stress treatment. However, all three populations exhibited similar trend in *A* during the period of water stress treatment in both cycles (Figures 5.3A and 5.3B). There were more significant differences in *A* among families within populations in both water stress

cycles (Tables 5.4 and 5.6). Both treatment by population interaction and treatment by family-within-population interaction were also significant on several days during the period of water stress treatment (Tables 5.4 and 5.6). Within each treatment (control and stress) these three populations also exhibited similar trend in *A* although the degree of response in *A* could vary on measurement date among populations during the period of water stress treatment (Figures 5.4A and 5.5A). Means of *A* are presented in Tables 5.7 and 5.8 for populations and in Tables 5.9 and 5.10 for families.

5.3.2 Transpiration

Similar to *A*, transpiration (*E*) of well-watered (control) seedlings was higher than that of water-stressed (stress) seedlings in both water stress cycles (Tables 5.3 and 5.5; Figures 5.2C and 5.2D). *E* of control seedlings varied from 1.75 to 3.26 mmol m^{-2} s^{-1} in cycle-1 (Table 5.3) and from 1.22 to 2.73 mmol m^{-2} s^{-1} in cycle-2 (Table 5.5).

In cycle-1, *E* of seedlings under water stress decreased from 1.78 mmol m^{-2} s^{-1} from Day 0 to less than 1.0 mmol m^{-2} s^{-1} on the second day (Day 2) of the water stress cycle (Table 5.3; Figure 5.2C). *E* of stress seedlings gradually decreased as water stress progressed and was relatively stable, at less than 0.4 mmol m^{-2} s^{-1}, during Day 7 to Day 10 of the water stress cycle (Table 5.3; Figure 5.2C). Although *E* of stress seedlings was significantly lower than *E* of control seedlings under water stress (Tables 5.3 and 5.4), *E* recovered when stress seedlings were rewatered. After 7 days of recovery from the 10-day water stress (Day 17), *E* of stress seedlings (2.36 mmol m^{-2} s^{-1}) was slightly lower than *E* of the control (2.70 mmol m^{-2} s^{-1}) (Table 5.3; Figure 5.2C).

In cycle-2, *E* of stress seedlings was significantly lower than *E* of control seedlings during the water stress (Tables 5.5 and 5.6). *E* of stress seedlings remained higher than 1.0 mmol m^{-2} s^{-1} during the early period of the water stress cycle and gradually decreased as water stress progressed (Figure 5.2D). After 10 days of water stress treatment, *E* was less than 0.4 mmol m^{-2} s^{-1} (Table 5.5). However, *E* of stress seedlings recovered rapidly following rewatering and after 7 days of recovery (Day 21), *E* of stress seedlings (1.60 mmol m^{-2} s^{-1}) was slightly lower than *E* of control seedlings (2.01 mmol m^{-2} s^{-1}) (Tables 5.5 and 5.6).

The transpiration rate of control seedlings among populations was more variable than that of water-stressed seedlings in both water stress cycles (Tables 5.7 and 5.8; Figures 5.4B and 5.5B). There were significant differences in *E* among populations and in treatment-by-population interaction on several sampling days in both water stress cycles (Tables 5.4 and 5.6). However, the trend of *E* among populations was similar during the period of water stress treatment although different degrees of response in *E* among populations were observed during the period of water stress treatment in both cycles (Figures 5.3C and 5.3D). Similarly, there were significant differences in *E* among families within populations and in treatment-by-family interaction on several sampling days in water-stressed cycle-1 (Table 5.4) and in water-stressed cycle-2 (Table 5.6). Means of *E* among families are presented in Tables 5.9 and 5.10.

5.3.3 Water-use efficiency

Water-use efficiency (WUE) of control seedlings was generally lower than WUE of stress seedlings in both water stress cycles (Tables 5.3 and 5.5; Figures 5.2E and 5.2F).

WUE of control seedlings was relatively consistent and ranged from 3.56 to 6.96 μmol CO_2/ mmol H_2O in cycle-1 (Table 5.3; Figure 5.2E) and from 4.19 to 9.91 μmol CO_2/ mmol H_2O in cycle-2 (Table 5.5; Figure 5.2F). On the other hand, WUE of stress seedlings increased at the onset of water stress (Figures 5.2E and 5.2F).

In cycle-1, WUE of stress seedlings gradually increased under mild water stress during the early period of the water stress treatment but decreased when severe water stress developed toward the end of water stress cycle (Table 5.3; Figure 5.2E). Generally, there were significant differences in WUE between control and stress seedlings during water stress treatment except on Day 10 (Tables 5.3 and 5.4). On the other hand, stress seedlings in cycle-2 maintained a significantly higher WUE than that of control seedlings under mild to moderate water stress but significantly decreased their WUE under severe stress (Tables 5.5 and 5.6; Figure 5.2F). However, seedlings under water stress recovered following rewatering. After 7 days of recovery, stress seedlings in cycle-1 (on Day 17) maintained as high WUE as that of control seedlings whereas stress seedlings in cycle-2 (on Day 21) had slightly higher WUE than that of control seedlings (Tables 5.3 and 5.5; Figures 5.2E and 5.2F).

Generally, WUE of stress seedlings was more variable among populations than WUE of control seedlings in both water stress cycles (Tables 5.7 and 5.8; Figures 5.4C and 5.5C). There were significant differences in WUE observed among populations and in treatment-by-population interaction on several sampling days during the water stress treatment in both cycles (Tables 5.4 and 5.6). These populations, however, exhibited the similar trend of WUE in both water stress cycles (Figures 5.3E and 5.3F). Although the degrees of response in WUE were different on some measurement date among

populations during the period of water stress treatment in both cycles, WUE among populations, generally, did not exhibit large differences (Figures 5.3E and 5.3F). In both water stress cycles, water-stressed seedlings generally increased their WUE under mild water stress but they decreased their WUE under severe water stress (Tables 5.7 and 5.8; Figures 5.4C and 5.5C). There were significant differences in WUE observed among families within populations on several days over the period of water stress treatment in both cycles (Tables 5.4 and 5.6). Treatment-by-family interaction was also significant on several sampling days during the period of water stress treatment in both cycles (Tables 5.4 and 5.6). Family means for WUE are also presented in Tables 5.9 and 5.10.

5.3.4 Water relations

Control seedlings maintained consistently high xylem water potential (Ψ_X) in both water stress cycles (Figures 5.2G and 5.2H). Ψ_X of the control was similar in both water stress cycles and ranged from −0.58 to −0.24 MPa in cycle-1 (Table 5.3) and from −0.44 to −0.24 MPa in cycle-2 (Table 5.5). Seedlings under water stress treatment also maintained high Ψ_X during the early period of water stress treatment and gradually decreased their Ψ_X as water stress progressively developed (Figures 5.2G and 5.2H).

In cycle-1, Ψ_X of the water-stressed seedlings was maintained as high as that of the control during the first 4 days of water stress treatment and gradually declined to be significantly lower than Ψ_X of the control for the rest period of the water stress cycle (Tables 5.3 and 5.4). After 10 days of the water stress treatment, water-stressed seedlings

recovered following rewatering and maintained a high Ψ_X (-0.55 MPa on Day 17) (Table 5.3).

In cycle-2, stress seedlings maintained high Ψ_X under water stress longer than that observed in the stress seedlings in cycle-1 (Figures 5.2G and 5.2H). Although Ψ_X of stressed seedlings was slightly lower than that of the control after the first 2 days of water stress treatment, Ψ_X of stress seedlings remained high during mild water stress and gradually declined as severe water stress developed (Table 5.5; Figure 5.2H). However, recovery from water stress was rapid following rewatering and after 7 days of recovery from 14 days of water stress (Day 21) Ψ_X of stressed seedlings (-0.35 MPa) was slightly lower than Ψ_X of the control (-0.24 MPa) (Table 5.5; Figure 5.2H).

There were significant differences in Ψ_X observed among populations in both water stress cycles (Tables 5.4 and 5.6). Similar to *A*, *E*, and WUE, Ψ_X also exhibited similar trend among populations although the degree of response in Ψ_X among populations were different during the period of water stress treatment (Figures 5.3G and 5.3H). However, Ψ_X among populations was more variable in cycle-1 (Figure 5.3G) than in cycle-2 (Figure 5.3H). Generally, seedlings from population 3 maintained higher Ψ_X than did seedlings from other two populations during the period of water stress treatment in both cycles (Figures 5.3G and 5.3H). This pattern was also observed for seedlings under water stress conditions in both cycles (Figures 5.4D and 5.5D). Control seedlings maintained Ψ_X that was relatively similar among populations throughout the water stress cycle whereas stressed seedlings exhibited variable Ψ_X among populations only under severe water stress (Tables 5.7 and 5.8; Figures 5.4D and 5.5D). Similarly, there were

significant differences in Ψ_X among families within populations observed in both water stress cycles under severe water stress (Tables 5.4 and 5.6). However, the treatment by family-within-population effect was not significant during the early period of water stress treatment but was significant as water stress progressively developed (Tables 5.4 and 5.6). Family means of Ψ_X in both water stress cycles are presented in Tables 5.9 and 5.10.

5.4 Discussion

The significant differences among populations and families within population in photosynthesis (*A*), transpiration (*E*), water-use efficiency (WUE) and xylem water potential (Ψ_X) observed in this study (Tables 5.4 and 5.6) agrees with the results of isozyme analysis (Chapter 2) and morphological and physiological studies (Chapter 4) which have revealed genetic variation among populations and families sampled from Thailand. However, significant differences among populations and families within population in *A*, *E*, WUE and Ψ_X were not observed on every sampling day during the period of water stress treatment. The different degrees of response in *A*, *E*, WUE and Ψ_X among populations over the period of water stress treatment in both water stress cycles in photosynthesis (Figures 5.3A and 5.3B), transpiration (Figures 5.3C and 5.3D), water-use efficiency (Figures 5.3E and 5.3F), and xylem water potential (Figures 5.3G and 5.3H) were responsible for the inconsistent significant differences among populations and families in these gas exchange and water relations over time (Tables 5.4 and 5.6). These populations exhibited rank changing during the period of water stress treatment in both water stress cycles (Figure 5.3). Similarly, seedlings grown under well-watered (control)

and water-stressed conditions also exhibited different response patterns and ranks among populations over the period of water stress treatment in photosynthesis, transpiration, water-use efficiency, and xylem water potential in both water stress cycles (Figures 5.4 and 5.5).

Among these four physiological parameters, xylem water potential (Ψ_X) exhibited relatively consistent response pattern and significant differences among populations over the period of water stress treatment in cycle-1 (Table 5.4; Figure 5.3G). Population 3, generally, maintained higher Ψ_X than did populations 1 and 2 (Figure 5.3G). Populations 1 and 2, as observed in other gas exchange parameters, also exhibited different response pattern and rank in Ψ_X among populations over the period of water stress treatment (Figure 5.3G). The higher Ψ_X in population 3 than in other two populations would probably reflect the influence of habitat characteristic. Population 3 represents the dry site (dry dipterocarp forest) whereas populations 1 and 2 represent moist habitat (mixed deciduous forest) (Table 5.1). Seedlings from population 3, therefore, would be capable of maintaining higher water potential than seedlings from the other two populations under water stress condition (Figure 5.3G). Tognetti et al. (1995) also observed higher water potentials in xeric populations than in mesic populations in European beech (*Fagus sylvatica* L.) seedlings during a drought cycle. However, there were less significant differences among populations in Ψ_X in cycle-2 water stress treatment (Table 5.6), although population 3 still, generally, maintained higher Ψ_X than did the other two populations (Figure 5.3H). Despite different response patterns in gas exchange and water relations observed among populations, *P. macrocarpus* seedlings, however, exhibited

similar trend in these physiological responses during the period of water stress treatment in both water stress cycles (Figures 5.3, 5.4 and 5.5).

Most physiological processes are complex and sensitive to the environments (Mahon 1983). The inconsistent differences among populations and families in these gas exchange and water relations observed over the period of water stress treatment in this study might also be due to the environmental sensitivity in these physiological parameters and variation among seedlings sampled on different days during the water stress treatment. Chaisurisri et al. (1998) also found significant differences among *P. macrocarpus* provenances in gas exchange parameters, but these differences represented only three percent of the total variation. Zine El Abidine et al. (1994) also observed small and inconsistent differences in gas exchange and water relations between black spruce seedlings from lowland and upland populations in response to water stress and concluded an absence of ecotypic variation with respect to drought resistance in this species. Zhang and Marshall (1994), however, did not detect differences in gas exchange and water-use efficiency among 14 populations of western larch seedlings under well-watered and water-stressed conditions. Abrams et al. (1990), studying green ash (*Fraxinus pennsylvanica* Marsh.), found that during drought seedlings from xeric habitats maintained higher photosynthetic rates than did seedlings from mesic habitats but their leaf water potentials were not significantly different. Tognetti et al. (1995), however, observed higher water potentials, photosynthesis and leaf conductance in xeric populations than in mesic populations in European beech seedlings during a drought cycle. It appears that response to drought is variable among different species (e.g., Ranney et al. 1990; Ni and Pallardy 1991; Reekie and Wayne 1992).

The degree of inhibition to photosynthesis also depended upon the degree of drought stress, and different species appear to differ in stress tolerance (McMichael 1980). For instance, net photosynthesis was completely inhibited at a leaf water potential of −11 bars in *Populus deltoides* Marsh. (Regehr et al. 1975) and at a leaf water potential of below −60 bars in *Acacia harpophylla* F. Muell. (van den Driessche et al. 1971). In this study, *P. macrocarpus* seedlings under well-watered conditions maintained relatively high *A* whereas the value for water-stressed seedlings was significantly lower during the water stress treatment (Tables 5.3 and 5.5; Figures 5.2A and 5.2B). During the 10-day period of water stress treatment in cycle-1, *A* of water-stressed seedlings declined from 9.73 μmol m^{-2} s^{-1} on Day 0 to only 1.49 μmol m^{-2} s^{-1} on Day 10 (Table 5.3). Photosynthesis seemed to be inhibited as soon as seedlings experienced only mild water stress (Figure 5.2A). Several studies in other species have shown that *A* gradually declines as water stress develops (e.g., Ceulemans et al. 1983; Abrams et al. 1990; Ni and Pallardy 1991; Tognetti et al. 1995). As drought develops, assimilation rate is reduced primarily by stomatal closure and increasing resistance to CO_2 diffusion (Schulze 1986). Drought stress can suspend or slow down the normal process of photosynthetic development (Ludlow and Ng 1974). Water stress was also reported to cause damage to photosynthetic apparatus (Kuhns et al. 1993) and increasing chlorophyll degradation (Michelozzi et al. 1995). It appears that the level of water stress imposed during the 10-day drought period in cycle-1 was not so severe as to cause any irreversible injury to seedlings. After rewatering and 7 days of recovery (Day 17), seedlings recovered from water stress and maintained a value of *A* (10.88 μmol m^{-2} s^{-1}) which is slightly lower than that (12.78 μmol m^{-2} s^{-1}) of control seedlings (Table 5.3; Figure 5.2A).

Similarly to *A*, transpiration (*E*) was also significantly affected by water limitations. In cycle-1, *E* of control seedlings remained relatively high whereas *E* of water-stressed seedlings decreased at the onset of water stress and stayed relatively low under moderate to severe water stress (Table 5.3; Figure 5.2C). These results suggest that stomata of *P. macrocarpus* are very sensitive to water deficits and stomatal closure or partial closure occurs even under mild water stress. Several studies have also reported similar patterns of stomatal sensitivity and response to mild water deficits (Buxton et al. 1985; Ranney et al. 1991; Edwards and Dixon 1995). The stomata act as plant protective mechanisms by decreasing water loss through closure during periods of plant water deficits (Jarvis 1980). However, stomatal closure will result not only in reduced water loss but also in reduced photosynthesis (Begg and Turner 1976). The reduction of both *A* and *E* was also observed in this study (Figures 5.2A and 5.2C).

WUE was also affected by water limitation but exhibited different patterns from *A* and *E* (Figures 5.2E and 5.2F). Seedlings under mild and moderate water stress increased and maintained a higher WUE than that of control plants. However, under severe water deficits, WUE of water-stressed seedlings declined. Increased WUE as water stress developed has been observed in several plant species. For instance, Ranney et al. (1990) found significant increases in WUE in response to water stress in *Acer negundo* L., and *Malus baccata* Barkh. Ni and Pallardy (1991) also observed an initial increase in WUE as the soil dried followed by a decline under severe water stress in some woody angiosperms. However, they did not observe any trend toward increased efficiency of water use in the more xeric species compared to a mesic species. Zhang and Marshall (1994), however, found no differences in WUE among western larch populations

although a higher WUE was observed in water-stressed seedlings than in well-watered seedlings.

Stewart et al. (1995) reported that mesophyll photosynthetic function was largely independent of water stress whereas stomatal conductance was sensitive to drought. Thus stomatal closure occurs before mesophyll photosynthetic function is greatly affected by water stress (Teskey et al. 1986). Initially photosynthesis declines as a result of stomatal closure, but prolonged and severe water stress can lead to depression of chloroplast and enzyme activity and to nonstomatal effects on photosynthesis (Begg and Turner 1976). WUE declined under severe water stress (Figures 5.2E and 5.2F) presumably because the development of nonstomatal inhibition of *A* exceeded the impact of reduction in stomatal conductance (Stewart et al. 1995). Different WUE among species, therefore, would reflect different strategies and abilities of plant species for drought resistance. High efficiency of water use is crucial not only for survival during seedling establishment (Cui and Smith 1991) but also for adapting to drier habitats (Monson and Grant 1989).

Resistance to drought among plant species depends on a variety of adaptive characteristics and mechanisms (Turner 1979; Ranney et al. 1990; Abrams 1994). These adaptations may enable plants either to maintain high tissue water potentials during drought (e.g., Reekie and Bazzaz 1989) or increase their tolerance of low water potentials (e.g., Ni and Pallardy 1991). Ranney et al. (1990) observed differences among species in water potentials at turgor loss point under severe stress condition, and the values ranged from −1.45 to −2.76 MPa. *P. macrocarpus* maintained relatively high xylem water potential (Ψ_X) under mild water stress during the early period of the water stress cycle

(Figures 5.2G and 5.2H) as a result of stomatal closure or partial closure which minimized transpirational water loss (Figures 5.2C and 5.2D). Maintenance of high Ψ_X under mild water stress would enable *P. macrocarpus* seedlings to resist water stress for a longer period as water stress progressively develops (Figures 5.2G and 5.2H). Under severe water stress *P. macrocarpus* seedlings maintained their Ψ_X lower than −1.7 MPa at 7-8% soil moisture content during Day 8 to Day 10 in cycle-1 (Tables 5.2 and 5.3). After a 10-day period of water stress, *P. macrocarpus* seedlings were able to recover from water stress following rewatering and maintained high Ψ_X (−0.55 MPa), *A* (10.88 μmol m^{-2} s^{-1}) and *E* (2.36 mmol m^{-2} s^{-1}) on Day 17 (Table 5.3). Maintenance of high Ψ_X during water deficits by stomatal closure and reducing *E* appears to be an effective mechanism for conserving water in *P. macrocarpus* seedlings and has been reported for other species in several studies (e.g., Ceulemans et al. 1983; Zine El Abidine et al. 1994; Edwards and Dixon 1995; Tognetti et al. 1995). Maintenance of high water potential at seedling stage is also crucial for survival to maturity (Cui and Smith 1991).

Several researchers have shown that drought preconditioning with repeated drying cycles improves plant tolerance to subsequent stress (e.g., Gebre and Kuhns 1993; Zine El Abidine et al. 1994; Edwards and Dixon 1995). In this study, the results suggested that water stress preconditioning improved the ability of *P. macrocarpus* seedlings to resist drought and maintain a higher level of gas exchange during water deficits although the benefit of water stress preconditioning through leaf physiological acclimation might be limited only in current growth season and would unlikely be extended to an other growth season because of it being a deciduous species. After a 7-day period of water stress

preconditioning, *P. macrocarpus* seedlings maintained relatively high *A* and *E* when subjected to the second water stress cycle (cycle-2) compared to those for seedlings in cycle-1 (Figures 5.2A, 5.2B, 5.2C and 5.2D). In cycle-2, *A* of stressed seedlings was maintained as high as that of control seedlings under mild water stress and gradually decreased as severe stress developed (Figure 5.2B). Similarly, *E* of stressed seedlings, although significantly lower than that of the control (Table 5.6; Figure 5.2D), was maintained at a higher level than *E* in cycle-1 under mild water stress and gradually decreased under severe stress (Figures 5.2C and 5.2D). WUE of stress seedlings in cycle-2 was also improved from that of stress seedlings observed in cycle-1 (Figures 5.2E and 5.2F) as a result of maintaining high *A* with minimal *E*. Improving WUE during water deficits also maintained high Ψ_X (Figures 5.2F and 5.2H). Stress preconditioned seedlings in cycle-2 maintained higher Ψ_X at lower soil moisture content compared to that observed in unconditioned seedlings in cycle-1 (Tables 5.2, 5.3, and 5.5). Ψ_X of stress seedlings in cycle-2 was -1.16 MPa at soil moisture content less than 7% on Day 12 (Tables 5.2 and 5.5) whereas Ψ_X of stress seedlings in cycle-1 was less than -1.7 MPa at 7-8% soil moisture content during Day 8 to Day 10 (Tables 5.2 and 5.3).

Decreased stomatal sensitivity to water deficits (Stewart et al. 1995) as indicated by transpiration rate would possibly be one of the physiological mechanisms involved in preconditioning observed in *P. macrocarpus* seedlings. Several studies have reported osmotic adjustment in plant tissue after plants are subjected to repeated drought cycles (e.g., Gebre and Kuhns 1993; Edwards and Dixon 1995). Because tissue osmotic potential was not investigated in this study, it was unknown if osmotic adjustment

occurred in *P. macrocarpus* seedlings. Munns (1988) postulated that species exhibiting reduced transpiration rates in response to drought showed little capacity to adjust osmotically. Zine El Abidine et al. (1994) found that preconditioning in black spruce seedlings occurred mostly through the acclimation of drought without active osmotic adjustment.

In conclusion, *P. macrocarpus* seedlings exhibited significant differences among populations and families within populations in gas exchange and water relations in response to water stress. Minimizing the transpiration loss of water by early stomatal closure and increasing efficiency of water use when experiencing only mild water deficits could maintain and prolong high tissue water status which is important for plants to survive a drought. Rapid recovery from drought conditions when water is available is also important for survival, especially in the field where soil moisture depends mainly on precipitation. *P. macrocarpus* seedlings also appear to benefit from water stress preconditioning which improved the ability of seedlings in drought tolerance.

P. macrocarpus is a deciduous species and sheds leaves during the dry season when soil moisture is limited. Hence acclimation through leaf morphological and physiological plasticity would be beneficial only during current year survival and growth. Chaisurisri et al. (1998) did not observe the benefit of drought stress preconditioning in term of post-planting survival and growth in *P. macrocarpus* seedlings after 1 and 2 years of planting in the field. Enhancing root growth therefore appears to be an associated important factor in drought tolerance (Tan et al. 1995) and would provide a longer term benefit to survival and growth under drought-prone environments. Nevertheless, acclimation of seedlings through water stress preconditioning to improve seedling

performance and resistance to drought remains important to seedling survival and establishment for this species. Such acclimation regime needs to be further developed. Genetic selection and improvement of both shoot and root growth associated with water stress preconditioning would therefore yield far more benefit for *P. macrocarpus* establishment on drought-prone sites.

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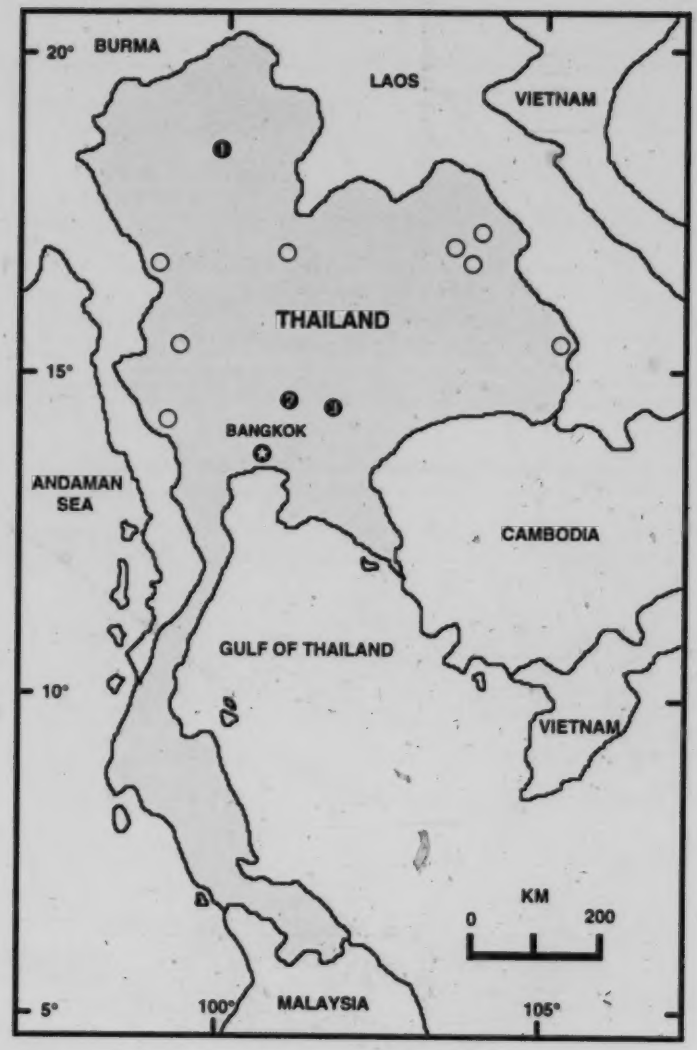

Figure 5.1 Map of Thailand showing locations of three populations of *P. macrocarpus* included in water stress study (●) and locations of other sampled populations (○).

Table 5.1 Geographic location, elevation, climate, forest type, and number of sampled trees of three populations of *P. macrocarpus* included in the water stress experiment.

Population No.	Name	Latitude (°N)	Longitude (°E)	Elevation (m)	Mean annual temperature (°C)	Annual rainfall (mm)	Forest type [a]	No. of sampled trees [b]
1	Lampang	18°35'	99°54'	350	25.9 [c]	1076.8 [c]	MDF	15 (6)
2	Saraburi	14°35'	101°12'	200	26.1 [d]	1168.0 [d]	MDF	33 (6)
3	Sakaerat	14°25'	101°45'	380	26.3 [e]	1310.0 [e]	DDF	106 (6)

[a] MDF: mixed deciduous forest (moist site); DDF: dry dipterocarp forest (dry site).

[b] Original number of sampled trees with size of subsample included in water stress experiment in parentheses.

[c] Meteorological Department, Bangkok, Thailand (1961-1990).

[d] Thai-Danish Dairy Farm, Saraburi, Thailand (1976-1990).

[e] Sakaerat Environmental Research Station, Nakhonratchasima, Thailand (1980-1989).

Table 5.2 Means ± SE (N = 18) of soil moisture content (% dry weight) of well-watered (control) and water-stressed (stress) treatments on each sampling day during the water stress experiment in *P. macrocarpus* seedlings.

Date	Days from last watering	Control	Stress
Cycle-1			
12-Apr-95	Day 0	24.69 ± 1.18	21.25 ± 0.93
14-Apr-95	Day 2	34.14 ± 1.63	16.67 ± 0.56
16-Apr-95	Day 4	35.09 ± 2.55	11.72 ± 0.57
18-Apr-95	Day 6	27.94 ± 2.37	9.15 ± 0.49
19-Apr-95	Day 7	40.29 ± 1.89	9.20 ± 0.53
20-Apr-95	Day 8	39.94 ± 2.39	8.09 ± 0.41
21-Apr-95	Day 9	41.09 ± 2.90	7.70 ± 0.54
22-Apr-95	Day 10	31.72 ± 2.32	7.80 ± 0.39
29-Apr-95	Day 17 [a]	48.96 ± 1.52	42.85 ± 1.23
Cycle-2			
26-Apr-95	Day 0	49.29 ± 1.58	48.86 ± 1.94
28-Apr-95	Day 2	44.44 ± 1.59	26.44 ± 1.58
30-Apr-95	Day 4	45.28 ± 1.33	16.69 ± 0.67
02-May-95	Day 6	48.14 ± 2.00	12.17 ± 0.59
04-May-95	Day 8	46.24 ± 1.96	10.77 ± 0.74
06-May-95	Day 10	44.06 ± 1.44	8.54 ± 0.49
08-May-95	Day 12	38.43 ± 1.70	6.36 ± 0.25
10-May-95	Day 14	30.52 ± 1.56	6.63 ± 0.29
17-May-95	Day 21 [b]	38.24 ± 2.17	31.49 ± 1.84

[a] 7-day recovery after 10-day water stress.
[b] 7-day recovery after 14-day water stress.

Table 5.3 Means ± SE (N = 36) of net photosynthesis (A, μmol m^{-2} s^{-1}), transpiration (E, mmol m^{-2} s^{-1}), water-use efficiency (WUE, μmol CO_2 /mmol H_2O) and xylem water potential (Ψ_X, MPa) of well-watered (control) and water-stressed (stress) *P. macrocarpus* seedlings in cycle-1 of the water stress experiment.

Days from last watering	Treatment	A	E	WUE	Ψ_X
Day 0	Control	11.57 ± 0.46	1.75 ± 0.09	6.96 ± 0.28	−0.55 ± 0.04
	Stress	9.73 ± 0.47	1.78 ± 0.10	5.62 ± 0.16	−0.47 ± 0.03
Day 2	Control	9.80 ± 0.51	1.87 ± 0.13	5.60 ± 0.23	−0.41 ± 0.03
	Stress	6.76 ± 0.31	0.98 ± 0.07	7.59 ± 0.38	−0.49 ± 0.03
Day 4	Control	11.81 ± 0.45	2.48 ± 0.13	5.01 ± 0.23	−0.49 ± 0.03
	Stress	5.44 ± 0.41	0.70 ± 0.04	8.13 ± 0.71	−0.54 ± 0.03
Day 6	Control	11.63 ± 0.53	2.76 ± 0.11	4.22 ± 0.10	−0.52 ± 0.04
	Stress	3.64 ± 0.38	0.50 ± 0.05	7.03 ± 0.36	−0.95 ± 0.10
Day 7	Control	11.31 ± 0.40	3.25 ± 0.13	3.56 ± 0.11	−0.51 ± 0.03
	Stress	2.85 ± 0.25	0.36 ± 0.03	7.94 ± 0.55	−1.05 ± 0.09
Day 8	Control	12.71 ± 0.52	3.26 ± 0.13	3.93 ± 0.09	−0.53 ± 0.03
	Stress	2.46 ± 0.30	0.39 ± 0.04	5.66 ± 0.34	−1.74 ± 0.16
Day 9	Control	10.41 ± 0.47	2.79 ± 0.14	3.93 ± 0.21	−0.58 ± 0.05
	Stress	1.79 ± 0.28	0.31 ± 0.04	5.49 ± 0.62	−1.85 ± 0.16
Day 10	Control	8.53 ± 0.52	2.38 ± 0.19	4.24 ± 0.41	−0.36 ± 0.03
	Stress	1.49 ± 0.18	0.33 ± 0.03	4.34 ± 0.35	−1.92 ± 0.18
Day 17 [a]	Control	12.78 ± 0.37	2.70 ± 0.11	4.94 ± 0.19	−0.24 ± 0.02
	Stress	10.88 ± 0.64	2.36 ± 0.18	5.01 ± 0.22	−0.55 ± 0.05

[a] 7-day recovery after 10-day water stress.

Table 5.4 Significance values for net photosynthesis (A, μmol m^{-2} s^{-1}), transpiration (E, mmol m^{-2} s^{-1}), water-use efficiency (WUE, μmol CO_2 /mmol H_2O) and xylem water potential (Ψ_x, MPa) in cycle-1 water stress experiment in *P. macrocarpus* seedlings.

			Days from last watering								
Parameter	Source	df	Day 0	Day 2	Day 4	Day 6	Day 7	Day 8	Day 9	Day 10	Day 17 [a]
A	Treatment	1	0.0021**	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0020**
	Population	2	0.0038**	0.4214	0.0625	0.4608	0.0970	0.5805	0.8989	0.0001**	0.3309
	Treatment * Population	2	0.3254	0.6415	0.3142	0.3941	0.0676	0.0152*	0.6382	0.0041**	0.2093
	Family (Population)	15	0.1203	0.0449*	0.0049**	0.0707	0.0001**	0.0005**	0.0140*	0.0007**	0.0066**
	Treatment * Family (Population)	15	0.1750	0.3223	0.0069**	0.0557	0.0001**	0.0058**	0.3020	0.0006**	0.0162*
	Error	36									
E	Treatment	1	0.8075	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0076**
	Population	2	0.0001**	0.1613	0.4256	0.1927	0.0199*	0.7272	0.2150	0.0016**	0.0046**
	Treatment * Population	2	0.8970	0.6281	0.2908	0.4813	0.0861	0.5761	0.0778	0.0067**	0.8349
	Family (Population)	15	0.4641	0.1549	0.1295	0.2344	0.0025**	0.0232*	0.9737	0.0687	0.0001**
	Treatment * Family (Population)	15	0.2282	0.3697	0.0661	0.3467	0.0145*	0.0168*	0.8880	0.0237*	0.0001**
	Error	36									
WUE	Treatment	1	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0219*	0.8426	0.7642
	Population	2	0.0053**	0.0001**	0.0306*	0.2949	0.1450	0.0557	0.2040	0.4281	0.0297*
	Treatment * Population	2	0.0569	0.0001**	0.3427	0.0094**	0.1428	0.0087**	0.1963	0.0355*	0.0096**
	Family (Population)	15	0.2555	0.0005**	0.0083**	0.0898	0.0001**	0.0345*	0.3994	0.4440	0.0679
	Treatment * Family (Population)	15	0.3694	0.0031**	0.0003**	0.0212*	0.0003**	0.1756	0.7063	0.0894	0.0016**
	Error	36									
Ψ_x	Treatment	1	0.1237	0.0631	0.2299	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**
	Population	2	0.0373*	0.0317*	0.0003**	0.0192*	0.0605	0.0001**	0.0038**	0.0001**	0.0264*
	Treatment * Population	2	0.8348	0.8674	0.1068	0.0013**	0.1142	0.0001**	0.5815	0.0001**	0.6031
	Family (Population)	15	0.8570	0.0443*	0.8505	0.0001**	0.5642	0.0001**	0.0001**	0.0001**	0.3360
	Treatment * Family (Population)	15	0.8560	0.1101	0.7495	0.0001**	0.5659	0.0001**	0.0001**	0.0001**	0.2751
	Error	36									

[a] 7-day recovery after 10-day water stress.
* significant at $P < 0.05$; ** significant at $P < 0.01$.

Table 5.5 Means ± SE (N = 36) of net photosynthesis (A, μmol m^{-2} s^{-1}), transpiration (E, mmol m^{-2} s^{-1}), water-use efficiency (WUE, μmol CO_2 /mmol H_2O) and xylem water potential (Ψ_X, MPa) of well-watered (control) and water-stressed (stress) *P. macrocarpus* seedlings in cycle-2 of the water stress experiment.

Days from last watering	Treatment	A	E	WUE	Ψ_X
Day 0	Control	12.78 ± 0.37	2.70 ± 0.11	4.94 ± 0.19	−0.24 ± 0.02
	Stress	12.89 ± 0.34	1.68 ± 0.07	8.07 ± 0.36	−0.28 ± 0.03
Day 2	Control	11.04 ± 0.38	2.73 ± 0.11	4.19 ± 0.17	−0.44 ± 0.04
	Stress	10.63 ± 0.51	1.90 ± 0.09	5.69 ± 0.22	−0.49 ± 0.05
Day 4	Control	12.24 ± 0.45	2.58 ± 0.10	4.80 ± 0.12	−0.36 ± 0.03
	Stress	11.46 ± 0.47	1.50 ± 0.08	7.96 ± 0.28	−0.49 ± 0.05
Day 6	Control	9.36 ± 0.50	1.87 ± 0.13	5.51 ± 0.27	−0.24 ± 0.01
	Stress	8.78 ± 0.56	1.23 ± 0.10	7.62 ± 0.35	−0.52 ± 0.05
Day 8	Control	11.66 ± 0.50	2.06 ± 0.11	5.85 ± 0.20	−0.31 ± 0.03
	Stress	8.19 ± 0.50	0.64 ± 0.05	13.80 ± 0.55	−0.50 ± 0.03
Day 10	Control	12.14 ± 0.51	1.62 ± 0.06	7.60 ± 0.21	−0.29 ± 0.02
	Stress	3.77 ± 0.37	0.25 ± 0.22	15.54 ± 1.29	−0.63 ± 0.11
Day 12	Control	11.81 ± 0.49	1.71 ± 0.10	7.30 ± 0.31	−0.39 ± 0.03
	Stress	4.03 ± 0.38	0.35 ± 0.03	11.67 ± 0.62	−1.16 ± 0.10
Day 14	Control	11.28 ± 0.56	1.22 ± 0.07	9.91 ± 0.53	−0.31 ± 0.01
	Stress	0.94 ± 0.55	0.29 ± 0.03	2.93 ± 0.28	−1.85 ± 0.17
Day 21 [a]	Control	11.44 ± 0.43	2.01 ± 0.09	5.86 ± 0.18	−0.24 ± 0.01
	Stress	10.64 ± 0.41	1.60 ± 0.08	6.86 ± 0.22	−0.35 ± 0.05

[a] 7-day recovery after 14-day water stress.

Table 5.6 Significance values for net photosynthesis (A, μmol m^{-2} s^{-1}), transpiration (E, mmol m^{-2} s^{-1}), water-use efficiency (WUE, μmol CO_2 /mmol H_2O) and xylem water potential (Ψ_x, MPa) in cycle-2 water stress experiment in *P. macrocarpus* seedlings.

			Days from last watering								
Parameter	Source	df	Day 0	Day 2	Day 4	Day 6	Day 8	Day 10	Day12	Day 14	Day 21 [a]
A	Treatment	1	0.8317	0.4978	0.1674	0.3889	0.0001**	0.0001**	0.0001**	0.0001**	0.1528
	Population	2	0.9338	0.2529	0.0387*	0.6955	0.0001**	0.3869	0.0302*	0.0581	0.4481
	Treatment * Population	2	0.9998	0.8869	0.4293	0.2856	0.0567	0.1436	0.1585	0.0074**	0.2637
	Family (Population)	15	0.2835	0.0261*	0.0303*	0.1062	0.0001**	0.0437*	0.0040**	0.0004**	0.1109
	Treatment * Family (Population)	15	0.3933	0.8934	0.3662	0.1242	0.0007**	0.2301	0.0809	0.0098**	0.2610
	Error	36									
E	Treatment	1	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0009**
	Population	2	0.0013**	0.1429	0.0401*	0.2233	0.0026**	0.7085	0.5928	0.0635	0.9221
	Treatment * Population	2	0.5169	0.1592	0.2835	0.0500*	0.0990	0.7061	0.3831	0.0393*	0.1863
	Family (Population)	15	0.0009**	0.1797	0.0075**	0.0134*	0.0246*	0.5803	0.0015**	0.0002**	0.3311
	Treatment * Family (Population)	15	0.0044**	0.4114	0.7249	0.3783	0.0159*	0.2223	0.0006**	0.1486	0.2605
	Error	36									
WUE	Treatment	1	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0004**
	Population	2	0.0006**	0.1022	0.2028	0.0630	0.0489*	0.1406	0.3805	0.0326*	0.9922
	Treatment * Population	2	0.4333	0.0734	0.6712	0.0857	0.0336*	0.0674	0.4744	0.0035**	0.1686
	Family (Population)	15	0.0018**	0.0334*	0.0044**	0.0001**	0.0541	0.0002**	0.6129	0.0002**	0.0220*
	Treatment * Family (Population)	15	0.1010	0.0173*	0.0500*	0.0033**	0.0079**	0.0001**	0.1025	0.0012**	0.5345
	Error	36									
Ψ_x	Treatment	1	0.2474	0.3167	0.0279*	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**	0.0017**
	Population	2	0.0012**	0.4036	0.0456*	0.0384*	0.0652	0.1805	0.3585	0.0001**	0.0071**
	Treatment * Population	2	0.9554	0.6908	0.2413	0.0955	0.6707	0.0889	0.0001**	0.0001**	0.1105
	Family (Population)	15	0.3043	0.0624	0.0733	0.4451	0.0342*	0.0020**	0.0001**	0.0001**	0.0004**
	Treatment * Family (Population)	15	0.1662	0.0925	0.7282	0.3561	0.0351*	0.0019**	0.0001**	0.0001**	0.0001**
	Error	36									

[a] 7-day recovery after 14-day water stress.
* significant at $P < 0.05$; ** significant at $P < 0.01$.

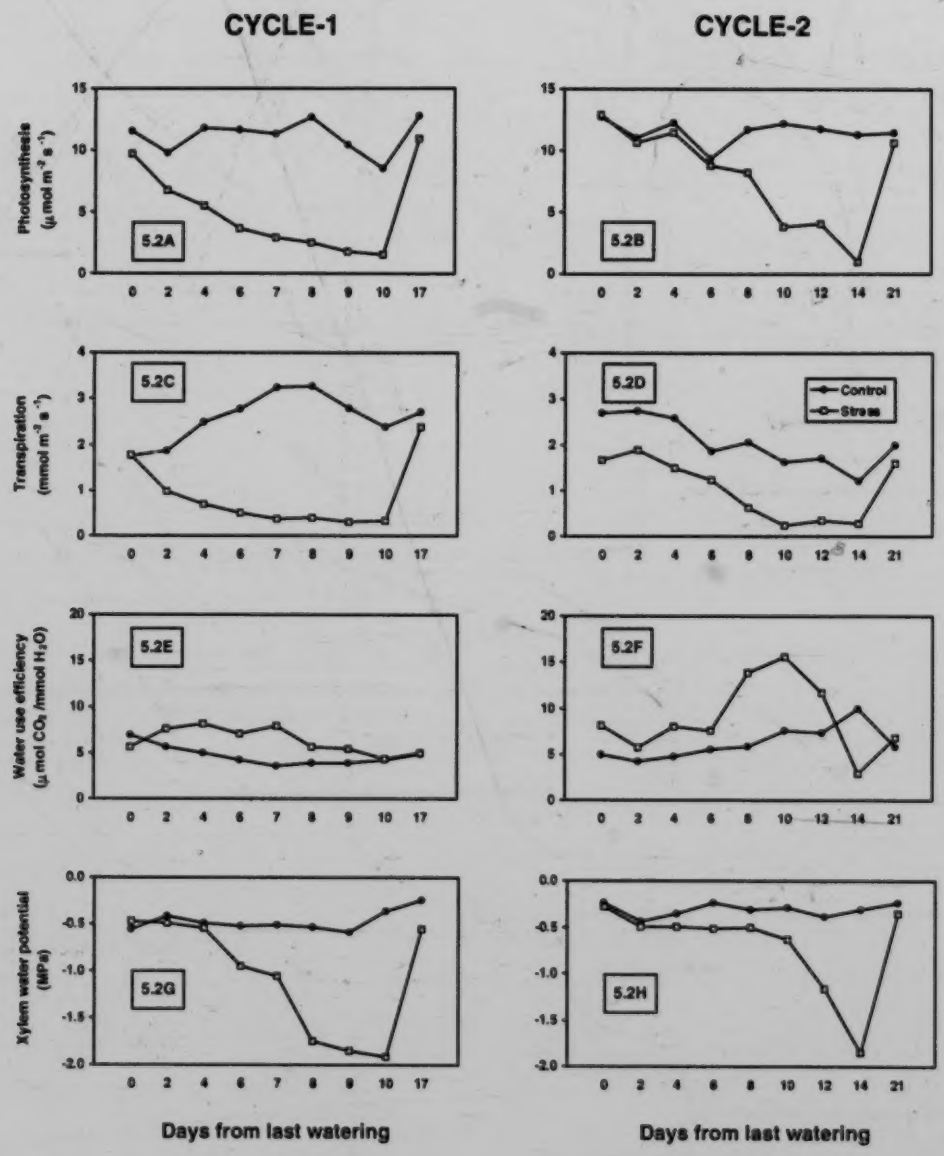

Figure 5.2 Patterns of photosynthesis, transpiration, water-use efficiency, and xylem water potential of *P. macrocarpus* seedlings under well-watered (control) and water-stressed (stress) conditions in cycle-1 and cycle-2 water stress experiment. Each symbol represents the mean of 36 seedlings pooled across three populations within each treatment. Error bars are not shown because they are smaller than the symbol.

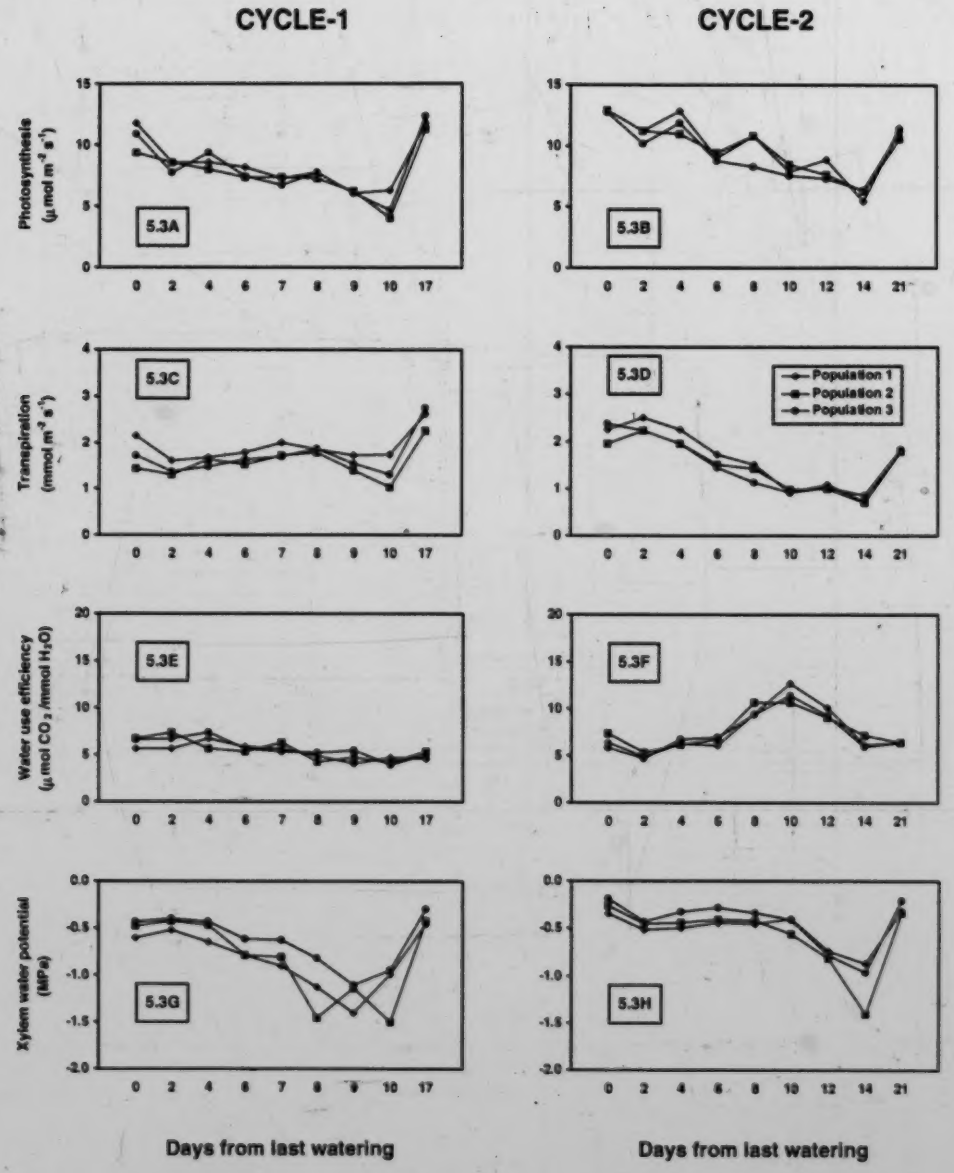

Figure 5.3 Patterns of photosynthesis, transpiration, water-use efficiency, and xylem water potential among populations of *P. macrocarpus* seedlings. Each symbol represents the mean of 24 seedlings pooled across well-watered (control) and water-stressed conditions within each population. Error bars are not shown because they are smaller than the symbol.

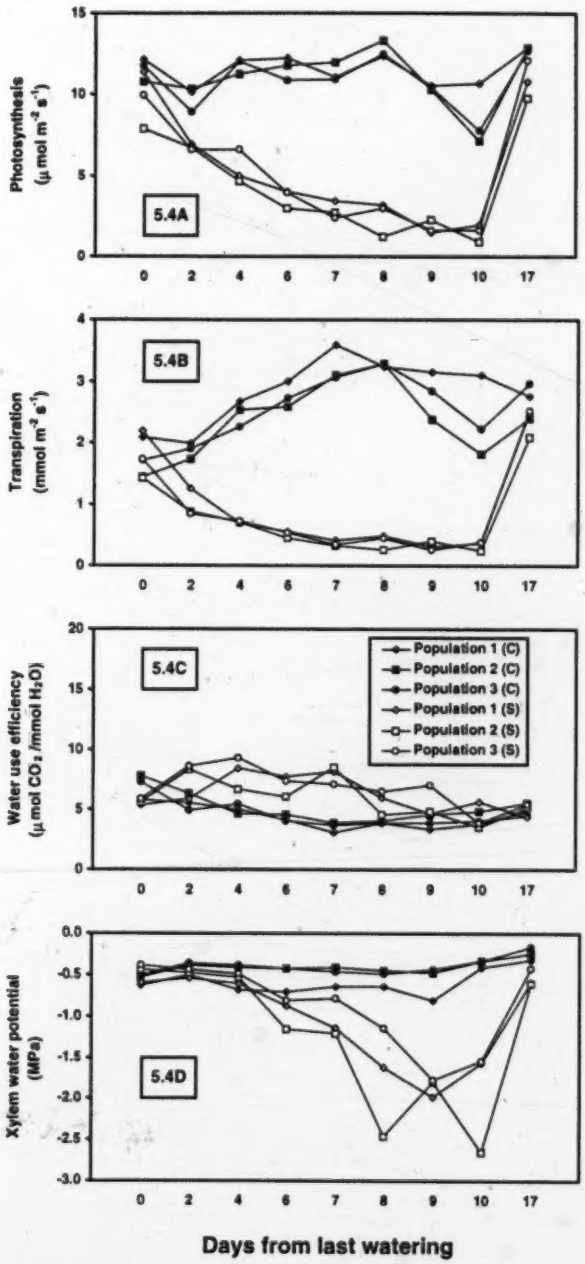

Figure 5.4 Patterns of photosynthesis, transpiration, water-use efficiency, and xylem water potential among populations of *P. macrocarpus* seedlings under well-watered or control (C) and water-stressed (S) conditions in cycle-1 water stress treatment. Each symbol represents the mean of 12 seedlings. Error bars are not shown because they are smaller than the symbol.

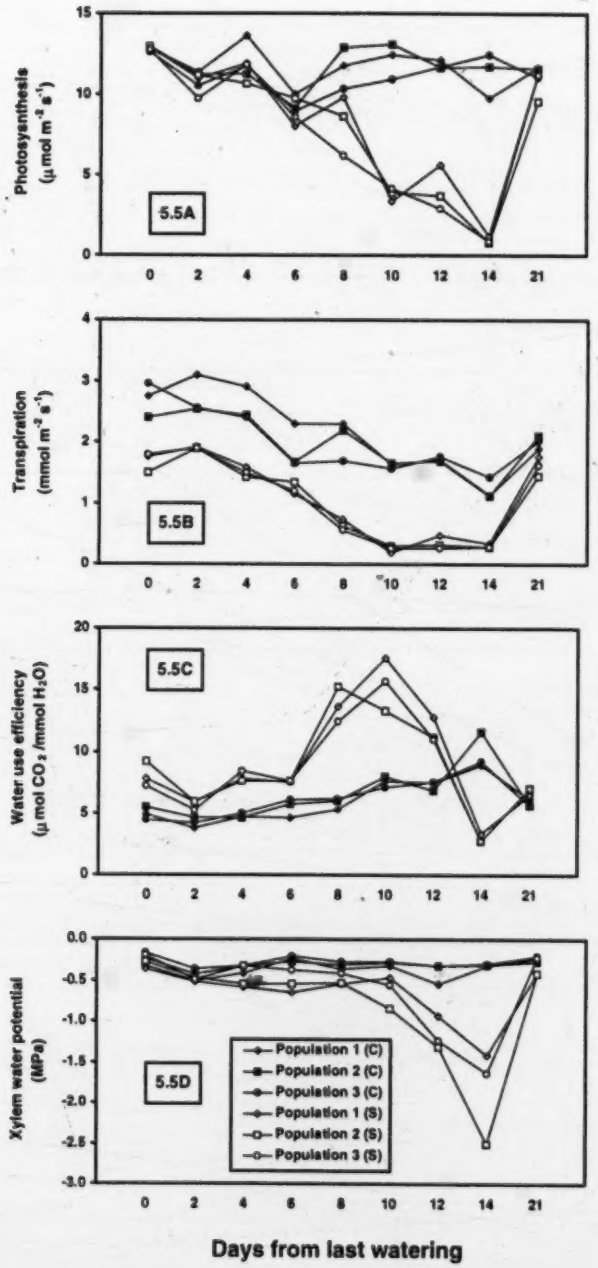

Figure 5.5 Patterns of photosynthesis, transpiration, water-use efficiency, and xylem water potential among populations of *P. macrocarpus* seedlings under well-watered or control (C) and water-stressed (S) conditions in cycle-2 water stress treatment. Each symbol represents the mean of 12 seedlings. Error bars are not shown because they are smaller than the symbol.

Table 5.7 Means ± SE (N = 12) of net photosynthesis (A, μmol m^{-2} s^{-1}), transpiration (E, mmol m^{-2} s^{-1}), water-use efficiency (WUE, μmol CO_2 /mmol H_2O) and xylem water potential (Ψ_x, MPa) of well-watered (control) and water-stressed (stress) *P. macrocarpus* seedlings among populations in cycle-1 of the water stress experiment.

Days from last watering	Population	A		E		WUE		Ψ_x	
		Control	Stress	Control	Stress	Control	Stress	Control	Stress
Day 0	1	12.18 ± 0.81	11.36 ± 0.67	2.09 ± 0.12	2.19 ± 0.17	5.83 ± 0.19	5.38 ± 0.38	−0.63 ± 0.07	−0.59 ± 0.06
	2	10.78 ± 0.85	7.89 ± 0.82	1.44 ± 0.14	1.42 ± 0.15	7.80 ± 0.52	5.61 ± 0.27	−0.53 ± 0.08	−0.44 ± 0.06
	3	11.75 ± 0.72	9.94 ± 0.64	1.71 ± 0.16	1.72 ± 0.13	7.24 ± 0.49	5.86 ± 1.60	−0.50 ± 0.05	−0.38 ± 0.04
Day 2	1	10.12 ± 0.80	6.94 ± 0.54	1.98 ± 0.25	1.24 ± 0.14	5.55 ± 0.40	5.84 ± 0.26	−0.50 ± 0.06	−0.54 ± 0.08
	2	10.33 ± 1.06	6.74 ± 0.27	1.73 ± 0.23	0.87 ± 0.08	6.35 ± 0.42	8.37 ± 0.63	−0.39 ± 0.05	−0.48 ± 0.05
	3	8.95 ± 0.80	6.59 ± 0.75	1.90 ± 0.21	0.83 ± 0.11	4.91 ± 0.28	8.56 ± 0.70	−0.36 ± 0.04	−0.44 ± 0.03
Day 4	1	12.12 ± 0.65	5.01 ± 0.63	2.66 ± 0.24	0.68 ± 0.07	4.97 ± 0.51	8.42 ± 1.85	−0.68 ± 0.05	−0.61 ± 0.06
	2	11.26 ± 1.03	4.68 ± 0.68	2.53 ± 0.25	0.70 ± 0.08	4.61 ± 0.38	6.67 ± 0.65	−0.41 ± 0.04	−0.53 ± 0.03
	3	12.04 ± 0.67	6.62 ± 0.77	2.25 ± 0.15	0.72 ± 0.07	5.46 ± 0.26	9.31 ± 0.81	−0.38 ± 0.04	−0.49 ± 0.06
Day 6	1	12.24 ± 1.10	4.02 ± 0.62	3.00 ± 0.22	0.54 ± 0.09	4.08 ± 0.18	7.68 ± 0.40	−0.71 ± 0.06	−0.88 ± 0.08
	2	11.77 ± 0.97	2.97 ± 0.66	2.58 ± 0.21	0.44 ± 0.09	4.59 ± 0.17	6.02 ± 0.70	−0.43 ± 0.05	−1.16 ± 0.19
	3	10.88 ± 0.67	3.93 ± 0.71	2.72 ± 0.13	0.53 ± 0.08	4.00 ± 0.15	7.39 ± 0.68	−0.42 ± 0.05	−0.81 ± 0.21
Day 7	1	11.07 ± 0.67	3.41 ± 0.55	3.59 ± 0.22	0.41 ± 0.05	3.11 ± 0.13	8.20 ± 0.61	−0.65 ± 0.07	−1.14 ± 0.20
	2	11.93 ± 0.77	2.73 ± 0.42	3.09 ± 0.20	0.33 ± 0.04	3.90 ± 0.19	8.55 ± 1.36	−0.41 ± 0.05	−1.21 ± 0.15
	3	10.94 ± 0.65	2.40 ± 0.29	3.06 ± 0.22	0.35 ± 0.04	3.66 ± 0.19	7.07 ± 0.73	−0.46 ± 0.04	−0.79 ± 0.06
Day 8	1	12.33 ± 1.03	3.16 ± 0.66	3.23 ± 0.24	0.48 ± 0.07	3.87 ± 0.22	5.97 ± 0.64	−0.65 ± 0.06	−1.62 ± 0.26
	2	13.31 ± 1.00	1.24 ± 0.25	3.28 ± 0.25	0.26 ± 0.04	4.07 ± 0.09	4.52 ± 0.62	−0.45 ± 0.04	−2.46 ± 0.30
	3	12.51 ± 0.72	2.98 ± 0.42	3.28 ± 0.18	0.45 ± 0.05	3.83 ± 0.11	6.48 ± 0.38	−0.49 ± 0.03	−1.14 ± 0.08
Day 9	1	10.54 ± 0.93	1.51 ± 0.31	3.14 ± 0.20	0.30 ± 0.03	3.34 ± 0.18	4.63 ± 0.77	−0.81 ± 0.11	−1.98 ± 0.17
	2	10.25 ± 0.87	2.26 ± 0.71	2.38 ± 0.22	0.39 ± 0.10	4.57 ± 0.51	4.80 ± 0.77	−0.48 ± 0.05	−1.80 ± 0.33
	3	10.44 ± 0.70	1.59 ± 0.33	2.84 ± 0.25	0.25 ± 0.04	3.87 ± 0.26	7.02 ± 1.46	−0.44 ± 0.04	−1.78 ± 0.32
Day 10	1	10.67 ± 0.67	1.95 ± 0.30	3.09 ± 0.28	0.36 ± 0.05	3.80 ± 0.42	5.65 ± 0.61	−0.41 ± 0.06	−1.57 ± 0.14
	2	7.13 ± 0.92	0.92 ± 0.24	1.81 ± 0.29	0.24 ± 0.03	4.86 ± 1.08	3.53 ± 0.63	−0.34 ± 0.04	−2.65 ± 0.32
	3	7.78 ± 0.82	1.60 ± 0.32	2.23 ± 0.34	0.38 ± 0.05	4.07 ± 0.46	3.84 ± 0.39	−0.34 ± 0.06	−1.55 ± 0.33
Day 17 *	1	12.84 ± 0.63	10.78 ± 1.03	2.75 ± 0.20	2.49 ± 0.26	4.87 ± 0.31	4.38 ± 0.31	−0.32 ± 0.05	−0.59 ± 0.07
	2	12.85 ± 0.49	9.78 ± 1.23	2.40 ± 0.15	2.08 ± 0.38	5.52 ± 0.31	5.17 ± 0.33	−0.24 ± 0.02	−0.61 ± 0.10
	3	12.65 ± 0.80	12.09 ± 1.26	2.95 ± 0.20	2.52 ± 0.45	4.44 ± 0.30	5.48 ± 0.45	−0.17 ± 0.02	−0.43 ± 0.07

* 7-day recovery after 10-day water stress.

Table 5.8 Means ± SE (N = 12) of net photosynthesis (A, μmol m^{-2} s^{-1}), transpiration (E, mmol m^{-2} s^{-1}), water-use efficiency (WUE, μmol CO_2 /mmol H_2O) and xylem water potential (Ψ_x, MPa) of well-watered (control) and water-stressed (stress) *P. macrocarpus* seedlings among populations in cycle-2 of the water stress experiment.

Days from last watering	Population	A		E		WUE		Ψ_x	
		Control	Stress	Control	Stress	Control	Stress	Control	Stress
Day 0	1	12.84 ± 0.63	12.96 ± 0.72	2.75 ± 0.20	1.75 ± 0.13	4.87 ± 0.31	7.84 ± 0.71	−0.32 ± 0.05	−0.37 ± 0.07
	2	12.85 ± 0.49	12.94 ± 0.34	2.40 ± 0.15	1.49 ± 0.13	5.52 ± 0.31	9.18 ± 0.64	−0.24 ± 0.02	−0.27 ± 0.05
	3	12.65 ± 0.80	12.75 ± 0.67	2.95 ± 0.20	1.79 ± 0.09	4.44 ± 0.30	7.19 ± 0.34	−0.17 ± 0.02	−0.20 ± 0.03
Day 2	1	11.39 ± 0.63	10.98 ± 0.94	3.10 ± 0.19	1.91 ± 0.17	3.75 ± 0.21	5.96 ± 0.52	−0.51 ± 0.07	−0.52 ± 0.11
	2	11.23 ± 0.86	11.18 ± 0.84	2.54 ± 0.21	1.90 ± 0.15	4.62 ± 0.38	5.93 ± 0.27	−0.43 ± 0.07	−0.47 ± 0.09
	3	10.51 ± 0.45	9.74 ± 0.90	2.55 ± 0.12	1.90 ± 0.17	4.21 ± 0.21	5.20 ± 0.30	−0.37 ± 0.04	−0.49 ± 0.07
Day 4	1	13.65 ± 0.93	11.91 ± 1.01	2.90 ± 0.20	1.58 ± 0.16	4.76 ± 0.20	7.78 ± 0.41	−0.42 ± 0.07	−0.59 ± 0.12
	2	11.28 ± 0.51	10.64 ± 0.68	2.44 ± 0.12	1.43 ± 0.12	4.68 ± 0.21	7.68 ± 0.43	−0.33 ± 0.04	−0.54 ± 0.08
	3	11.79 ± 0.69	11.83 ± 0.70	2.41 ± 0.13	1.49 ± 0.14	4.95 ± 0.23	8.42 ± 0.60	−0.33 ± 0.06	−0.33 ± 0.03
Day 6	1	10.00 ± 0.90	8.03 ± 1.01	2.29 ± 0.24	1.15 ± 0.22	4.62 ± 0.27	7.59 ± 0.40	−0.23 ± 0.02	−0.65 ± 0.10
	2	9.13 ± 0.98	9.76 ± 0.93	1.67 ± 0.20	1.33 ± 0.13	5.78 ± 0.45	7.64 ± 0.73	−0.27 ± 0.02	−0.54 ± 0.07
	3	8.95 ± 0.74	8.55 ± 0.97	1.65 ± 0.22	1.21 ± 0.18	6.12 ± 0.57	7.63 ± 0.66	−0.21 ± 0.03	−0.38 ± 0.07
Day 8	1	11.76 ± 0.99	9.77 ± 0.87	2.29 ± 0.24	0.73 ± 0.08	5.36 ± 0.28	13.67 ± 0.43	−0.36 ± 0.08	−0.55 ± 0.06
	2	12.91 ± 0.37	8.59 ± 0.86	2.19 ± 0.12	0.63 ± 0.10	6.01 ± 0.23	15.25 ± 1.22	−0.31 ± 0.03	−0.53 ± 0.04
	3	10.33 ± 0.98	6.21 ± 0.52	1.69 ± 0.13	0.55 ± 0.08	6.18 ± 0.46	12.48 ± 0.94	−0.27 ± 0.05	−0.42 ± 0.06
Day 10	1	12.42 ± 0.97	3.33 ± 0.60	1.64 ± 0.11	0.20 ± 0.02	7.68 ± 0.43	17.62 ± 3.04	−0.33 ± 0.05	−0.47 ± 0.15
	2	13.08 ± 0.73	3.85 ± 0.68	1.65 ± 0.10	0.30 ± 0.05	8.01 ± 0.30	13.34 ± 1.68	−0.28 ± 0.03	−0.85 ± 0.26
	3	10.94 ± 0.88	4.13 ± 0.68	1.57 ± 0.13	0.26 ± 0.04	7.11 ± 0.34	15.67 ± 1.72	−0.27 ± 0.03	−0.56 ± 0.12
Day 12	1	12.12 ± 0.82	5.56 ± 0.64	1.70 ± 0.14	0.47 ± 0.07	7.43 ± 0.50	12.83 ± 1.00	−0.54 ± 0.04	−0.94 ± 0.09
	2	11.62 ± 0.80	3.67 ± 0.72	1.68 ± 0.09	0.32 ± 0.05	6.89 ± 0.31	11.20 ± 1.22	−0.33 ± 0.04	−1.31 ± 0.27
	3	11.71 ± 0.97	2.87 ± 0.37	1.75 ± 0.26	0.27 ± 0.04	7.58 ± 0.73	10.99 ± 1.00	−0.32 ± 0.04	−1.24 ± 0.12
Day 14	1	9.71 ± 0.89	1.20 ± 0.23	1.13 ± 0.10	0.33 ± 0.03	8.94 ± 0.86	3.37 ± 0.43	−0.33 ± 0.03	−1.41 ± 0.23
	2	11.70 ± 1.03	0.78 ± 0.24	1.11 ± 0.14	0.28 ± 0.06	11.62 ± 1.10	2.71 ± 0.64	−0.31 ± 0.02	−2.51 ± 0.35
	3	12.44 ± 0.91	0.83 ± 0.26	1.43 ± 0.13	0.28 ± 0.06	9.16 ± 0.60	2.73 ± 0.40	−0.30 ± 0.02	−1.63 ± 0.22
Day 21 *	1	11.67 ± 0.71	11.16 ± 0.74	1.90 ± 0.10	1.75 ± 0.14	6.20 ± 0.27	6.50 ± 0.33	−0.23 ± 0.02	−0.42 ± 0.10
	2	11.58 ± 0.72	9.56 ± 0.58	2.11 ± 0.16	1.44 ± 0.14	5.67 ± 0.35	7.02 ± 0.46	−0.27 ± 0.03	−0.41 ± 0.11
	3	11.06 ± 0.87	11.20 ± 0.76	2.03 ± 0.19	1.62 ± 0.11	5.70 ± 0.34	7.06 ± 0.37	−0.21 ± 0.03	−0.22 ± 0.03

* 7-day recovery after 14-day water stress.

Table 5.9 Means (N = 2) of net photosynthesis (*A*, μmol m^{-2} s^{-1}), transpiration (*E*, mmol m^{-2} s^{-1}), water-use efficiency (WUE, μmol CO_2 /mmol H_2O) and xylem water potential (Ψ_x, MPa) of well-watered (control) and water-stressed (stress) *P. macrocarpus* seedlings among families in cycle-1 of the water stress experiment.

		A		*E*		WUE		Ψ_x	
Population	Family	Control	Stress	Control	Stress	Control	Stress	Control	Stress
Day 0									
1	5	15.50	9.25	2.40	1.55	6.52	5.98	-0.725	-0.500
1	7	13.55	10.85	2.40	1.75	5.64	6.32	-0.575	-0.525
1	9	12.75	13.75	2.15	2.05	5.95	6.80	-0.650	-0.675
1	10	9.15	13.85	1.65	3.15	5.61	4.45	-0.550	-0.775
1	14	10.55	11.30	2.05	2.40	5.13	4.71	-0.675	-0.525
1	15	11.60	9.15	1.90	2.25	6.13	4.02	-0.625	-0.538
2	72	14.25	9.50	2.15	1.70	6.63	5.49	-0.400	-0.325
2	73	10.10	8.75	1.40	1.30	7.88	6.73	-0.400	-0.338
2	74	7.05	8.25	1.15	1.60	6.66	5.21	-0.700	-0.500
2	77	12.30	8.00	1.35	1.55	9.33	5.29	-0.475	-0.313
2	81	10.05	4.30	1.30	0.80	7.82	5.38	-0.675	-0.400
2	86	10.95	8.55	1.30	1.55	8.50	5.58	-0.500	-0.750
3	110	12.00	9.30	1.65	1.65	7.82	5.67	-0.575	-0.325
3	119	11.00	8.65	1.80	1.80	6.85	4.93	-0.350	-0.438
3	120	10.45	10.40	1.60	1.70	6.57	6.12	-0.400	-0.500
3	131	13.05	8.35	1.35	1.35	9.70	6.19	-0.763	-0.400
3	135	9.85	9.10	1.85	1.45	5.43	6.29	-0.500	-0.400
3	139	14.15	13.85	2.00	2.35	7.08	5.93	-0.438	-0.225
Day 2									
1	5	12.05	8.75	2.15	1.75	5.81	5.15	-0.575	-0.700
1	7	11.90	8.25	2.15	1.55	6.31	5.85	-0.263	-0.650
1	9	10.80	5.05	2.80	0.85	3.88	5.95	-0.450	-0.775
1	10	6.80	7.85	0.95	1.25	7.18	6.25	-0.500	-0.400
1	14	10.05	5.90	2.05	1.10	5.03	5.37	-0.825	-0.425
1	15	9.10	5.85	1.80	0.95	5.09	6.47	-0.375	-0.300
2	72	11.55	7.80	1.45	1.10	8.03	7.12	-0.450	-0.675
2	73	16.20	7.85	2.75	1.25	5.88	6.36	-0.275	-0.300
2	74	7.75	5.90	1.05	0.55	7.38	10.85	-0.625	-0.625
2	77	6.05	6.00	1.25	0.95	4.92	6.32	-0.150	-0.413
2	81	11.60	6.20	2.65	0.70	4.51	8.94	-0.313	-0.438
2	86	8.85	6.70	1.20	0.65	7.37	10.63	-0.525	-0.425
3	110	6.85	7.65	1.90	0.80	3.86	9.71	-0.300	-0.475
3	119	9.00	4.85	1.90	0.75	4.69	6.45	-0.525	-0.350
3	120	10.10	5.60	2.00	0.60	5.50	10.60	-0.300	-0.450
3	131	6.85	6.15	1.25	0.65	5.58	9.55	-0.350	-0.450
3	135	10.45	6.30	1.85	1.20	5.65	5.24	-0.375	-0.525
3	139	10.45	9.00	2.50	1.00	4.17	9.80	-0.288	-0.375
Day 4									
1	5	11.60	2.75	1.65	0.65	7.19	3.96	-0.675	-0.638
1	7	13.10	7.15	2.40	0.95	5.46	7.42	-0.650	-0.675
1	9	14.00	4.55	3.50	0.85	4.00	5.42	-0.725	-0.388
1	10	13.35	4.20	1.95	0.65	6.81	6.49	-0.725	-0.700
1	14	11.75	7.60	3.60	0.45	3.31	19.58	-0.725	-0.750
1	15	8.90	3.80	2.85	0.50	3.07	7.67	-0.600	-0.500
2	72	15.15	5.30	2.70	1.00	5.60	5.31	-0.425	-0.413
2	73	12.25	2.10	3.35	0.40	3.67	5.40	-0.525	-0.550
2	74	10.45	4.35	2.95	0.70	3.57	6.21	-0.375	-0.600
2	77	6.55	4.55	1.65	0.70	4.06	6.46	-0.475	-0.475
2	81	10.00	3.35	2.60	0.65	3.94	5.32	-0.300	-0.675
2	86	13.15	8.45	1.95	0.75	6.83	11.22	-0.375	-0.475
3	110	11.55	9.75	2.80	0.90	4.13	11.12	-0.550	-0.475
3	119	11.20	5.20	2.10	0.65	5.34	7.96	-0.375	-0.575
3	120	14.35	7.35	2.55	0.70	5.76	10.69	-0.425	-0.425
3	131	11.50	4.85	2.00	0.50	5.75	9.79	-0.225	-0.475
3	135	9.55	9.45	1.95	0.95	5.06	11.17	-0.375	-0.625
3	139	14.10	3.10	2.10	0.60	6.71	5.17	-0.350	-0.350

Table 5.9 Continued.

Population	Family	*A*		*E*		WUE		Ψ_x	
		Control	Stress	Control	Stress	Control	Stress	Control	Stress
Day 6									
1	5	16.05	2.30	3.60	0.35	4.46	6.63	-0.675	-0.975
1	7	13.15	7.50	2.95	1.05	4.43	7.39	-0.750	-0.575
1	9	11.05	2.60	2.70	0.30	4.06	8.38	-0.750	-1.175
1	10	10.65	3.90	2.55	0.60	4.16	6.51	-0.525	-0.775
1	14	9.45	4.40	3.05	0.60	3.09	7.23	-0.975	-0.725
1	15	13.10	3.40	3.15	0.35	4.19	9.95	-0.563	-1.075
2	72	15.40	3.90	3.65	0.45	4.23	8.55	-0.625	-1.050
2	73	9.10	3.60	1.85	0.45	4.96	7.25	-0.488	-1.125
2	74	7.05	1.10	1.85	0.25	3.81	4.25	-0.500	-0.800
2	77	11.25	5.35	2.60	0.90	4.39	6.01	-0.413	-0.388
2	81	13.75	0.30	2.60	0.10	5.29	3.00	-0.275	-2.225
2	86	14.05	3.55	2.90	0.50	4.87	7.06	-0.288	-1.350
3	110	10.65	0.65	2.75	0.10	3.81	6.50	-0.363	-2.275
3	119	13.35	3.70	3.15	0.60	4.32	6.17	-0.650	-0.513
3	120	8.80	7.65	2.65	0.75	3.33	10.25	-0.225	-0.275
3	131	9.15	2.50	2.30	0.30	3.98	8.33	-0.325	-0.775
3	135	11.60	4.80	2.65	0.60	4.38	7.80	-0.625	-0.600
3	139	11.70	4.25	2.80	0.80	4.18	5.32	-0.325	-0.450
Day 7									
1	5	15.15	5.60	4.30	0.60	3.55	9.33	-0.725	-0.663
1	7	9.25	2.10	3.05	0.30	3.08	7.00	-0.775	-1.400
1	9	12.35	4.05	4.55	0.55	2.77	7.27	-0.525	-0.775
1	10	9.60	2.50	3.40	0.40	2.82	6.83	-0.875	-1.325
1	14	9.20	5.20	3.15	0.45	2.93	11.50	-0.575	-0.825
1	15	10.85	1.00	3.10	0.15	3.50	7.25	-0.438	-1.875
2	72	14.60	3.20	2.80	0.35	5.21	10.60	-0.700	-1.163
2	73	11.85	3.50	3.40	0.40	3.50	8.75	-0.275	-1.050
2	74	7.15	4.00	1.90	0.25	3.76	16.17	-0.263	-1.050
2	77	14.45	2.45	3.75	0.45	3.86	5.30	-0.325	-0.925
2	81	12.40	0.45	3.60	0.15	3.45	3.50	-0.413	-1.725
2	86	11.15	2.80	3.10	0.40	3.61	7.00	-0.488	-1.350
3	110	13.05	2.60	3.35	0.25	3.99	10.67	-0.438	-1.038
3	119	9.80	1.15	3.45	0.25	2.88	5.17	-0.588	-0.850
3	120	11.65	3.35	3.60	0.40	3.27	8.50	-0.525	-0.700
3	131	7.65	2.40	2.05	0.35	3.74	6.88	-0.450	-0.425
3	135	11.35	1.40	3.25	0.30	3.49	4.75	-0.288	-0.900
3	139	12.15	3.50	2.65	0.55	4.61	6.43	-0.500	-0.813
Day 8									
1	5	16.90	4.45	3.55	0.60	4.79	7.42	-0.625	-1.050
1	7	14.20	6.55	3.95	0.85	3.62	7.66	-0.388	-0.700
1	9	12.85	0.35	3.80	0.20	3.39	1.75	-0.588	-3.250
1	10	7.65	2.20	2.10	0.40	3.72	5.50	-0.600	-1.775
1	14	11.65	4.05	3.00	0.60	4.01	6.76	-0.800	-1.175
1	15	10.70	1.35	2.95	0.20	3.63	6.75	-0.913	-1.750
2	72	16.25	1.10	4.05	0.20	4.02	5.50	-0.450	-2.663
2	73	9.60	1.45	2.35	0.35	4.09	4.17	-0.475	-1.738
2	74	8.70	2.50	2.05	0.45	4.25	5.45	-0.513	-1.188
2	77	16.35	0.45	3.85	0.15	4.25	2.50	-0.538	-3.600
2	81	14.10	0.50	3.45	0.15	4.11	3.75	-0.375	-3.600
2	86	14.85	1.45	3.90	0.25	3.80	5.75	-0.338	-2.000
3	110	12.00	2.40	3.10	0.40	3.86	5.80	-0.413	-1.375
3	119	11.50	4.40	2.95	0.60	4.06	7.33	-0.513	-1.150
3	120	14.70	2.65	3.60	0.35	4.09	7.75	-0.438	-0.950
3	131	12.65	1.90	3.20	0.30	3.93	6.33	-0.450	-1.263
3	135	13.80	5.10	3.65	0.75	3.78	6.79	-0.538	-0.775
3	139	10.40	1.45	3.15	0.30	3.27	4.83	-0.600	-1.350

Table 5.9 Continued.

Population	Family	*A*		*E*		WUE		Ψ_x	
		Control	Stress	Control	Stress	Control	Stress	Control	Stress
Day 9									
1	5	14.20	1.50	3.35	0.25	4.21	6.50	-0.813	-2.163
1	7	9.85	0.60	3.50	0.15	2.79	3.00	-0.600	-2.575
1	9	11.45	1.95	3.15	0.40	3.64	4.90	-1.200	-1.050
1	10	7.70	0.55	2.75	0.25	2.84	2.17	-0.325	-2.200
1	14	8.40	3.30	2.60	0.45	3.27	7.38	-1.250	-1.975
1	15	11.65	1.15	3.50	0.30	3.30	3.83	-0.675	-1.925
2	72	9.00	1.95	2.10	0.35	4.31	5.38	-0.575	-1.363
2	73	12.30	6.95	2.15	1.00	6.98	7.13	-0.463	-0.500
2	74	8.20	1.40	2.30	0.25	3.87	5.83	-0.388	-1.975
2	77	11.50	1.25	2.60	0.20	4.36	6.25	-0.563	-1.650
2	81	7.60	0.00	2.20	0.10	3.47	0.00	-0.300	-3.938
2	86	12.90	2.00	2.90	0.45	4.46	4.25	-0.588	-1.350
3	110	11.80	1.65	3.30	0.25	3.66	6.33	-0.375	-1.150
3	119	8.00	0.35	2.30	0.20	4.21	1.75	-0.413	-2.950
3	120	11.15	3.15	2.30	0.45	4.83	7.00	-0.313	-0.913
3	131	13.00	1.60	3.40	0.25	3.82	10.00	-0.650	-0.750
3	135	8.40	2.00	3.00	0.25	2.80	9.00	-0.450	-1.475
3	139	10.30	0.80	2.75	0.10	3.92	8.00	-0.413	-3.425
Day 10									
1	5	10.60	0.95	3.20	0.30	3.40	3.00	-0.375	-1.638
1	7	9.70	1.55	2.85	0.25	3.40	6.50	-0.275	-2.200
1	9	12.20	2.85	3.95	0.45	3.10	6.45	-0.338	-1.563
1	10	12.05	0.85	3.40	0.15	3.58	6.50	-0.850	-1.575
1	14	7.45	2.60	1.90	0.60	5.61	4.17	-0.288	-0.738
1	15	12.00	2.90	3.25	0.40	3.70	7.25	-0.350	-1.700
2	72	3.85	0.00	1.00	0.20	3.92	0.00	-0.438	-3.950
2	73	8.45	0.85	2.20	0.20	3.81	4.25	-0.300	-1.975
2	74	4.85	0.60	1.45	0.15	3.37	4.50	-0.250	-2.450
2	77	11.10	2.10	3.15	0.40	3.52	5.20	-0.350	-1.388
2	81	5.45	1.55	1.40	0.30	4.48	5.25	-0.200	-2.075
2	86	9.10	0.40	1.65	0.20	10.07	2.00	-0.500	-4.075
3	110	4.90	0.60	1.20	0.30	4.25	2.00	-0.750	-1.838
3	119	6.00	2.45	1.25	0.55	6.07	4.46	-0.275	-1.250
3	120	7.50	2.15	1.80	0.40	4.24	5.38	-0.150	-0.538
3	131	8.10	1.25	2.80	0.30	2.89	4.17	-0.375	-1.313
3	135	13.05	0.35	4.15	0.15	3.15	2.50	-0.225	-3.750
3	139	7.15	2.80	2.15	0.60	3.80	4.51	-0.275	-0.613
Day 17 [a]									
1	5	14.65	12.45	2.35	3.30	6.23	3.77	-0.425	-0.363
1	7	11.55	5.80	2.30	1.10	5.02	4.19	-0.425	-0.700
1	9	15.80	12.65	3.70	2.35	4.27	5.39	-0.275	-0.500
1	10	12.10	12.20	3.35	2.50	3.65	4.87	-0.163	-0.725
1	14	12.20	9.85	2.90	3.20	4.27	3.11	-0.413	-0.575
1	15	10.75	11.70	1.90	2.50	5.72	4.91	-0.225	-0.700
2	72	14.35	12.70	3.15	2.25	4.62	5.69	-0.225	-0.200
2	73	13.55	13.60	1.90	3.75	7.18	3.67	-0.325	-0.425
2	74	12.65	9.10	2.30	1.75	5.48	5.21	-0.288	-0.925
2	77	13.65	6.10	2.75	1.20	4.94	5.59	-0.300	-0.800
2	81	11.70	12.20	2.35	2.70	5.09	4.55	-0.113	-0.613
2	86	11.20	5.00	1.95	0.80	5.75	6.20	-0.200	-0.700
3	110	12.70	13.20	3.50	2.00	3.71	7.14	-0.250	-0.450
3	119	10.50	15.90	2.00	3.40	5.32	4.65	-0.188	-0.475
3	120	12.10	14.70	2.60	3.15	4.78	4.66	-0.225	-0.500
3	131	12.75	4.50	3.55	0.70	3.58	6.55	-0.125	-0.325
3	135	14.95	10.15	2.80	1.55	5.34	6.55	-0.125	-0.700
3	139	12.90	14.10	3.25	4.30	3.94	3.27	-0.113	-0.150

[a] 7-day recovery after 10-day water stress.

Table 5.10 Means (N = 2) of net photosynthesis (*A*, μmol m^{-2} s^{-1}), transpiration (*E*, mmol m^{-2} s^{-1}), water-use efficiency (WUE, μmol CO_2 /mmol H_2O) and xylem water potential (Ψ_X, MPa) of well-watered (control) and water-stressed (stress) *P. macrocarpus* seedlings among families in cycle-2 of the water stress experiment.

		A		*E*		WUE		Ψ_X	
Population	Family	Control	Stress	Control	Stress	Control	Stress	Control	Stress
Day 0									
1	5	14.65	15.90	2.35	1.40	6.23	11.36	-0.425	-0.225
1	7	11.55	11.45	2.30	1.30	5.02	8.81	-0.425	-0.525
1	9	15.80	12.95	3.70	1.90	4.27	6.83	-0.275	-0.300
1	10	12.10	10.25	3.35	1.95	3.65	5.53	-0.163	-0.613
1	14	12.20	13.50	2.90	2.35	4.27	5.73	-0.413	-0.400
1	15	10.75	13.70	1.90	1.60	5.72	9.03	-0.225	-0.175
2	72	14.35	12.90	3.15	1.45	4.62	8.97	-0.225	-0.250
2	73	13.55	11.65	1.90	1.45	7.18	8.04	-0.325	-0.175
2	74	12.65	12.55	2.30	2.10	5.48	6.70	-0.288	-0.500
2	77	13.65	14.55	2.75	1.25	4.94	12.05	-0.300	-0.150
2	81	11.70	12.25	2.35	1.35	5.09	9.05	-0.113	-0.250
2	86	11.20	13.75	1.95	1.35	5.74	10.21	-0.200	-0.313
3	110	12.70	10.05	3.50	1.55	3.71	6.54	-0.250	-0.100
3	119	10.50	15.20	2.00	2.25	5.32	6.74	-0.188	-0.200
3	120	12.10	11.85	2.60	1.65	4.78	7.20	-0.225	-0.300
3	131	12.75	12.80	3.55	1.95	3.58	6.71	-0.125	-0.325
3	135	14.95	12.70	2.80	1.55	5.34	8.20	-0.125	-0.125
3	139	12.90	13.95	3.25	1.80	3.94	7.74	-0.125	-0.163
Day 2									
1	5	11.95	13.85	3.70	1.60	3.23	8.78	-0.725	-1.300
1	7	12.75	13.75	3.65	2.00	3.49	6.88	-0.350	-0.300
1	9	10.20	7.75	2.50	1.65	4.19	4.62	-0.350	-0.475
1	10	8.05	7.75	2.40	1.75	3.35	4.72	-0.388	-0.425
1	14	12.75	11.70	3.75	2.00	3.40	6.18	-0.550	-0.375
1	15	12.65	11.10	2.60	2.45	4.86	4.50	-0.725	-0.250
2	72	13.80	12.45	2.45	1.70	5.52	7.37	-0.575	-0.250
2	73	8.80	8.60	2.10	1.60	4.16	5.38	-0.325	-0.550
2	74	9.90	12.25	2.20	2.30	5.61	5.33	-0.625	-0.475
2	77	13.40	12.35	3.20	2.40	4.25	5.16	-0.250	-0.350
2	81	10.20	8.85	2.60	1.55	3.97	5.56	-0.325	-0.788
2	86	11.25	12.55	2.70	1.85	4.17	6.80	-0.450	-0.388
3	110	9.90	7.30	2.15	1.65	4.61	4.41	-0.300	-0.825
3	119	8.95	11.25	2.50	2.45	3.74	4.58	-0.325	-0.413
3	120	9.30	6.80	2.85	1.40	3.28	4.90	-0.600	-0.300
3	131	11.20	9.60	2.25	1.60	4.99	6.14	-0.300	-0.638
3	135	12.75	10.40	2.70	1.70	4.72	6.12	-0.325	-0.450
3	139	10.95	13.10	2.85	2.60	3.84	5.04	-0.375	-0.325
Day 4									
1	5	17.15	14.15	3.40	2.10	5.06	6.85	-0.575	-1.000
1	7	15.30	13.50	3.60	1.45	4.26	9.30	-0.338	-0.300
1	9	13.85	11.75	3.20	2.00	4.34	5.90	-0.450	-0.650
1	10	9.50	5.90	1.95	0.75	4.74	7.80	-0.288	-0.750
1	14	12.55	13.80	2.95	1.65	4.24	8.73	-0.625	-0.600
1	15	13.55	12.35	2.30	1.55	5.86	8.08	-0.225	-0.250
2	72	8.60	10.75	2.15	1.45	4.02	7.40	-0.250	-0.500
2	73	11.75	12.45	2.70	1.85	4.36	6.73	-0.275	-0.475
2	74	10.45	13.20	2.35	1.55	4.51	9.38	-0.288	-0.275
2	77	12.75	9.00	2.75	1.10	4.64	8.30	-0.325	-0.600
2	81	12.60	9.60	2.60	1.35	5.04	7.34	-0.500	-0.450
2	86	11.55	8.85	2.10	1.30	5.50	6.84	-0.350	-0.950
3	110	11.85	10.15	2.85	1.80	4.15	6.07	-0.175	-0.188
3	119	10.60	12.25	2.65	1.90	4.03	6.45	-0.413	-0.375
3	120	12.80	13.30	2.25	1.65	5.68	8.24	-0.150	-0.263
3	131	9.45	12.70	1.85	1.15	4.96	11.08	-0.650	-0.438
3	135	13.95	9.30	2.60	1.10	5.37	8.75	-0.213	-0.350
3	139	12.10	13.25	2.25	1.35	5.44	9.96	-0.400	-0.350

Table 5.10 Continued.

Population	Family	*A*		*E*		WUE		Ψ_x	
		Control	Stress	Control	Stress	Control	Stress	Control	Stress
Day 6									
1	5	12.70	10.35	3.10	1.35	4.10	7.92	-0.250	-0.525
1	7	12.15	7.05	2.45	0.75	5.04	9.42	-0.225	-0.375
1	9	8.85	8.80	2.20	1.20	4.11	7.27	-0.150	-0.875
1	10	5.25	3.60	0.85	0.45	6.24	7.92	-0.275	-0.850
1	14	9.20	11.00	2.35	2.00	3.98	6.58	-0.250	-0.800
1	15	11.85	7.35	2.80	1.15	4.26	6.41	-0.225	-0.488
2	72	10.65	6.25	1.95	1.20	5.31	5.47	-0.275	-0.525
2	73	11.55	9.65	2.05	1.45	5.57	6.59	-0.250	-0.650
2	74	7.25	10.40	1.15	1.05	6.98	10.04	-0.275	-0.525
2	77	6.60	12.90	1.20	1.15	5.39	11.35	-0.363	-0.725
2	81	9.00	10.85	2.35	1.45	3.84	7.37	-0.225	-0.600
2	86	9.70	8.50	1.30	1.70	7.53	5.02	-0.250	-0.225
3	110	11.10	7.80	2.30	1.10	4.84	7.21	-0.188	-0.200
3	119	9.05	13.10	1.90	2.25	4.80	5.94	-0.250	-0.350
3	120	10.15	10.10	1.35	1.40	7.96	7.32	-0.163	-0.300
3	131	10.55	6.40	2.00	1.10	6.01	6.29	-0.325	-0.200
3	135	7.95	4.15	1.75	0.60	4.55	6.93	-0.150	-0.475
3	139	4.90	9.75	0.60	0.80	8.56	12.04	-0.188	-0.750
Day 8									
1	5	13.20	12.45	2.55	1.05	5.20	11.92	-0.750	-0.475
1	7	9.00	11.55	1.25	0.90	7.17	12.93	-0.163	-0.425
1	9	15.75	10.05	3.25	0.75	4.81	13.35	-0.513	-0.525
1	10	7.70	10.65	1.45	0.75	5.35	14.44	-0.250	-0.500
1	14	14.35	9.70	2.95	0.65	5.02	14.88	-0.225	-0.525
1	15	10.55	4.20	2.30	0.30	4.60	14.50	-0.238	-0.838
2	72	13.50	12.35	2.15	1.10	6.37	11.53	-0.163	-0.325
2	73	13.20	10.10	2.20	0.90	6.20	11.26	-0.350	-0.513
2	74	12.80	7.20	2.55	0.45	5.23	16.03	-0.350	-0.513
2	77	11.30	10.35	1.95	0.70	5.82	14.67	-0.275	-0.475
2	81	14.15	6.25	2.30	0.40	6.15	16.03	-0.350	-0.725
2	86	12.50	5.30	2.00	0.25	6.25	22.00	-0.363	-0.650
3	110	7.25	5.10	1.50	0.35	4.86	14.88	-0.213	-0.625
3	119	9.60	4.85	1.90	0.45	5.10	10.65	-0.400	-0.475
3	120	8.80	7.50	1.75	0.50	5.24	15.42	-0.500	-0.300
3	131	13.80	5.05	2.10	0.75	6.65	10.02	-0.125	-0.263
3	135	7.80	6.20	1.25	0.50	6.21	12.40	-0.200	-0.638
3	139	14.70	8.55	1.65	0.75	8.97	11.51	-0.200	-0.200
Day 10									
1	5	12.10	4.45	1.75	0.25	6.94	17.33	-0.250	-0.188
1	7	11.35	1.70	1.55	0.20	7.28	8.50	-0.338	-1.500
1	9	15.50	6.25	1.85	0.25	8.37	24.33	-0.275	-0.400
1	10	11.05	1.45	1.25	0.20	8.90	7.25	-0.225	-0.400
1	14	11.75	3.55	2.00	0.10	5.70	35.50	-0.625	-0.200
1	15	12.75	2.55	1.45	0.20	8.77	12.75	-0.250	-0.150
2	72	14.00	3.70	1.85	0.40	7.59	9.67	-0.275	-0.438
2	73	11.40	4.75	1.35	0.30	8.70	18.38	-0.425	-0.650
2	74	13.15	8.15	1.45	0.55	9.05	16.25	-0.263	-0.200
2	77	15.45	2.30	2.05	0.20	7.55	11.50	-0.200	-0.800
2	81	9.65	1.80	1.40	0.20	6.88	9.00	-0.325	-2.350
2	86	14.80	2.40	1.80	0.15	8.23	15.25	-0.175	-0.650
3	110	9.05	7.15	1.25	0.45	7.25	15.95	-0.250	-0.325
3	119	9.05	0.90	1.25	0.15	7.18	5.50	-0.213	-1.300
3	120	12.50	6.60	1.65	0.35	7.49	18.88	-0.238	-0.213
3	131	10.20	3.35	1.65	0.20	6.82	16.75	-0.400	-0.325
3	135	10.00	3.65	1.70	0.20	5.88	21.17	-0.338	-0.500
3	139	14.85	3.15	1.90	0.20	8.03	15.75	-0.175	-0.700

Table 5.10 Continued.

Population	Family	*A*		*E*		WUE		Ψ_x	
		Control	Stress	Control	Stress	Control	Stress	Control	Stress
Day 12									
1	5	13.85	8.45	2.05	0.70	6.92	12.07	-0.400	-0.675
1	7	9.10	5.20	1.05	0.45	8.64	11.48	-0.475	-0.800
1	9	15.35	4.70	1.70	0.30	9.23	17.50	-0.613	-1.200
1	10	13.45	3.25	2.15	0.25	6.24	13.08	-0.575	-1.063
1	14	9.15	3.75	1.85	0.30	4.96	12.75	-0.675	-1.200
1	15	11.80	8.00	1.40	0.80	8.47	10.00	-0.475	-0.675
2	72	10.65	7.20	1.50	0.55	7.06	13.17	-0.275	-0.775
2	73	14.10	6.35	1.80	0.55	7.99	11.67	-0.425	-0.825
2	74	10.00	2.95	1.80	0.25	5.58	12.67	-0.338	-1.250
2	77	12.55	3.15	1.70	0.30	7.39	10.50	-0.375	-0.788
2	81	10.00	0.60	1.50	0.10	6.60	6.00	-0.288	-3.250
2	86	12.40	1.75	1.80	0.15	6.71	13.25	-0.263	-1.000
3	110	9.50	2.60	1.20	0.25	7.80	10.67	-0.488	-0.950
3	119	14.35	4.75	2.30	0.40	6.28	13.92	-0.225	-1.000
3	120	10.95	2.00	1.60	0.20	7.40	10.00	-0.288	-1.350
3	131	10.50	1.30	1.05	0.20	11.04	6.50	-0.450	-1.938
3	135	15.45	2.80	3.20	0.20	4.81	14.00	-0.163	-1.325
3	139	9.50	3.75	1.15	0.35	8.19	10.92	-0.300	-0.850
Day 14									
1	5	9.90	0.75	0.85	0.30	12.41	2.50	-0.313	-1.350
1	7	15.05	2.00	1.45	0.40	10.42	5.00	-0.263	-1.025
1	9	10.50	1.90	1.30	0.45	8.61	4.13	-0.175	-0.750
1	10	7.70	1.10	1.00	0.35	7.75	2.35	-0.463	-0.700
1	14	7.30	0.60	1.20	0.20	6.08	3.00	-0.375	-1.950
1	15	7.80	0.85	1.00	0.25	8.43	3.17	-0.363	-2.675
2	72	14.70	2.20	1.75	0.70	8.73	3.17	-0.413	-0.775
2	73	15.75	0.90	1.40	0.25	11.35	3.58	-0.275	-1.600
2	74	12.25	1.00	1.10	0.15	11.17	6.00	-0.263	-2.225
2	77	9.30	0.30	0.90	0.20	10.12	1.50	-0.313	-3.825
2	81	8.75	0.20	0.45	0.15	19.08	1.75	-0.200	-3.625
2	86	9.45	0.05	1.05	0.20	9.28	0.25	-0.388	-3.000
3	110	8.85	0.70	0.70	0.15	12.67	4.75	-0.388	-2.250
3	119	11.80	0.20	1.35	0.15	8.88	1.50	-0.325	-2.500
3	120	16.80	0.25	1.60	0.10	10.68	2.50	-0.275	-1.475
3	131	11.20	0.30	1.55	0.20	7.24	1.50	-0.225	-1.875
3	135	11.20	2.45	1.45	0.60	7.72	4.04	-0.288	-0.775
3	139	14.80	1.10	1.90	0.50	7.79	2.05	-0.300	-0.875
Day 21 [a]									
1	5	13.75	13.85	2.05	2.05	6.74	6.79	-0.263	-0.275
1	7	9.45	10.20	1.85	1.70	5.21	5.96	-0.200	-0.225
1	9	12.95	13.90	2.25	2.45	5.71	5.68	-0.250	-0.125
1	10	9.00	8.40	1.35	1.40	6.69	6.13	-0.188	-0.875
1	14	12.25	9.80	2.00	1.60	6.13	6.29	-0.225	-0.775
1	15	12.60	10.80	1.90	1.30	6.64	8.25	-0.263	-0.225
2	72	12.45	9.90	2.25	1.40	5.69	7.07	-0.275	-0.150
2	73	12.70	7.85	2.25	0.80	5.84	9.88	-0.225	-0.275
2	74	11.40	8.40	2.60	1.35	4.37	6.22	-0.225	-1.150
2	77	13.65	9.95	1.85	1.30	7.50	7.69	-0.200	-0.275
2	81	7.75	9.80	1.35	1.80	5.72	5.52	-0.250	-0.325
2	86	11.55	11.45	2.35	2.00	4.97	5.73	-0.450	-0.275
3	110	10.30	8.80	2.25	1.35	5.52	6.65	-0.250	-0.250
3	119	10.35	9.80	2.40	1.50	4.39	6.64	-0.200	-0.425
3	120	11.15	12.20	1.95	1.70	5.71	7.62	-0.175	-0.138
3	131	12.40	11.80	2.10	1.75	5.79	6.93	-0.263	-0.163
3	135	7.70	14.15	1.30	1.90	6.04	7.52	-0.225	-0.200
3	139	14.45	10.45	2.15	1.50	6.71	7.00	-0.125	-0.150

[a] 7-day recovery after 14-day water stress.

CHAPTER 6

CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

The major aim of this dissertation was to investigate the level and distribution of genetic variation in natural populations of *Pterocarpus macrocarpus*. Open-pollinated seeds were collected from 287 families from 11 natural populations throughout Thailand. Isozyme analysis was employed to investigate the pattern of genetic variation and mating system for these 11 populations (Chapters 2 and 3). Nursery grown seedlings from 112 families from six populations were also evaluated for genetic variation in growth, morphological and physiological traits for a 30-week growth period (Chapter 4). In addition, seedlings from 18 families from three populations were also investigated for gas exchange and water relations in response to water stress (Chapter 5). The results of these studies revealed that *P. macrocarpus* exhibited genetic variation in isozymes, morphological traits and physiological parameters.

P. macrocarpus from Thailand possesses a high level of genetic variation. Although a large portion of isozyme variation resides within populations, 12.1% of the total genetic variation resides among populations. This level of population differentiation is also comparable to that reported for other tropical tree species (Hamrick 1994). *P. macrocarpus* has a large natural distribution covering several countries in southeast Asia (Rojo 1977). The species is also predominantly outcrossing with average outcrossing rate of greater than 0.8 (t_s = 0.819 and t_m = 0.899, Chapter 3). Widespread distribution and a predominantly outcrossing mode could be factors attributable to the high level of genetic

variation in *P. macrocarpus* (Hamrick et al. 1991; Bawa 1994). Cluster analysis using Nei's (1972) genetic distance also revealed a geographic pattern of isozyme variation. These 11 populations exhibited an east-west pattern of population grouping which was in accord with significant correlations between allelic frequencies and longitudes at eight loci.

Genetic variation in seedling growth and morphological traits was also detected among populations and families within populations. Generally, the percentage of total variation due to families within populations was relatively larger than that due to populations. This pattern of quantitative variation conformed to that of isozyme variation, which revealed 87% of total variation resided within populations. In contrast to isozyme variation, there was no apparent geographic pattern in growth and morphological variation among six populations included in the nursery study. The environment of seed origin appeared to have a partial influence on seedling growth performance. Although seedling survival after the 30-week growth period was similar among populations, seedlings from populations with climatic conditions similar to the growth conditions in the nursery generally performed better than seedlings from populations where climatic conditions were dissimilar. Strikingly, seedlings derived from seeds collected from the location where the nursery study was carried out performed the best.

Significant variation among families within populations was also detected for photosynthesis, transpiration and water-use efficiency. However, only water-use efficiency exhibited significant differences among populations. Similar to growth and morphological traits, there was no apparent geographic pattern in these physiological

parameters among these six populations. The pattern of physiological variation, however, appeared to conform with the pattern of growth and morphological variation.

A moderate to high level of genetic control and genetic correlations among growth and morphological traits suggests the opportunity for genetic improvement and early genetic selection for these growth and morphological traits. In contrast, the potential use of physiology in genetic improvement, as a basis for early selection, appears to be limited due to the lack of simple relationship between physiological parameters and growth performance. However, physiological acclimation is possible to improve early survival and growth under drought-prone sites through water stress preconditioning. Although there were significant differences among populations and families within populations, the similar trend in physiological responses to water stress of *P. macrocarpus* seedlings among populations implies the need of similar acclimation regime for this species.

The pattern of genetic variation between isozyme markers and quantitative traits is inconsistent. In some studies, agreement between variation in isozymes and variation in other quantitative traits has been reported (e.g., Knowles and Grant 1981; Hamrick 1983; Linhart and Mitton 1985). Other studies, however, have failed to demonstrate the presence of association or concordance between isozyme data and quantitative traits (e.g., Wheeler and Guries 1982; El-Kassaby 1982; Furnier et al. 1991; Kjær et al. 1996). In this study, only isozymes revealed a longitudinal geographic pattern of population grouping. It is generally assumed that isozyme loci may be selectively neutral or nearly neutral (Kimura 1983). Thus, it is not known if genetic differentiation inferred from isozyme studies is indicative of a selective advantage or disadvantage. Lewontin (1984) has demonstrated that significant differences among the frequencies of individual loci

affecting a quantitative trait are more difficult to demonstrate than differences in the quantitative traits itself. He also concluded that generalization of isozyme studies to other traits of evolutionary significance could be misleading. Hattemer (1991) also pointed out that patterns of variation at non-neutral loci may differ from those of neutral loci. As a result of these considerations one would expect more genetic differentiation among populations for traits which are undergoing diversifying selection. Therefore, changes of adaptive characters are likely to go undetected because of the low correlation in level and pattern of variation between isozymes and adaptive characters (Savolainen and Kärkkäinen 1992).

For the conservation of forest genetic resources, the maximum procurement of variation at gene loci and the maintenance of specific adaptive gene complexes are two prime objectives (Brown 1979). In this study, the prominent longitudinal differentiation of populations suggests that an optimal strategy for *ex situ* conservation of *P. macrocarpus* in Thailand would be to sample seeds from a few trees in each of many populations to include a wide spectrum across the east-west environment. Populations that exhibit significant genetic differentiation would be the obvious targets for sampling. In addition, germplasm collections in *P. macrocarpus* should also include materials from other countries to assure adequate sampling of the genome for conservation. However, extended investigation of patterns of genetic variation to cover the whole range of the species is required for developing proper sampling strategy.

Low outcrossing rates would imply limited pollen movement or gene flow among individuals within a population. Thus, in a population where the degree of habitat disturbance is high and population density is low, such as some eastern *P. macrocarpus*

populations in Thailand, sampling from these populations which were associated with low outcrossing rates should include more trees to ensure sufficient sampling of genetic variability.

Genetic variation in quantitative traits also provides useful implications for genetic conservation and genetic improvement in *P. macrocarpus*. The observed environmental influence on quantitative variation suggests that plantations for *ex situ* conservation and for seed and wood production should include materials from populations which have environmental climates similar to the planting sites in order to maintain adaptation and maximize growth performance. In this regard, seed deployment zones need to be developed. The preliminary seed deployment zones for *P. macrocarpus* in Thailand would possibly be broadly defined into three regions. These include (1) northern region, (2) northeastern region, and (3) central and western region. Because Thailand is located in the middle of *P. macrocarpus* natural range, each region would possibly be extended to cover *P. macrocarpus* populations from adjacent countries. However, information on quantitative variation from more populations, more test sites and more growth seasons throughout a species range is needed for such development.

Similar to *ex situ* conservation, longitudinal geographic patterns of population differentiation also suggest that, for *in situ* conservation, natural populations of *P. macrocarpus* should be sampled along the east-west distribution range. Ideally, as many *P. macrocarpus* populations as possible should be included in the conservation program. However, several constraints, such as operational funds and manpower, limit such ideal operations. In addition, forest resources in Thailand have also been under consistent threats by encroachment and shifting cultivation of rural inhabitants and illegal logging.

Hence, the success of *in situ* conservation, therefore, depends not only on effective genetic sampling strategies but also on effective protection of the resources. Priorities for conservation, therefore, should be assigned to the existing protected areas, such as national parks and wildlife sanctuaries where *P. macrocarpus* naturally occurs. The cluster analysis (Figure 2.2, Chapter 2) which revealed four separate geographic regions also suggests that forest reserves should be sampled from all four regions. Within each region, populations with a high level of genetic diversity should be given a priority for conservation.

P. macrocarpus naturally occurs in association with other tree species (Komkris 1965; Bunyavejchewin 1983). It would be more effective and with a high cost benefit to design protected areas that include other associated species. However, to effectively design and define reserves that include many associated species requires information about pattern of genetic variation in other associated species. In the study of *Dalbergia cochinchinensis*, Soonhuae (1993) also observed a geographic trend for isozyme variation among eight populations sampled from central and northeastern Thailand. If the geographic pattern of isozyme variation in other species, which would be included in the same *in situ* conservation, corresponds with each other, *in situ* conservation would be simplified. However, such information currently is rarely available.

The patterns of genetic variation in *P. macrocarpus* in this thesis were studied from populations sampled only in Thailand. Many of these populations are remnant and disturbed, particularly populations from the east. The level of genetic variation detected from Thai populations, therefore, would possibly be lower than that for populations in other neighbouring countries, such as Burma, Laos and Cambodia, where *P. macrocarpus*

populations would likely be less disturbed and more continuous. Extensive investigation of the pattern of genetic variation to cover the whole species range would provide the accurate information regarding the level of genetic variation in this species. The east-west trend of population grouping observed in this study also poses an interesting question if this east-west trend continues throughout the species range or it only exhibits among populations in Thailand. This information will be very useful for genetic resource management and conservation of *P. macrocarpus* for the entire species range. The immediate benefit would be to restore genetic diversity in some of the Thai populations, such as eastern populations, using germplasms from adjacent neighbouring countries.

6.2 Recommendations for further study

1. Because only materials from Thailand were included in this study, further study on the pattern of genetic variation to include samples from other countries across the whole natural range of *P. macrocarpus* is a prerequisite to effective development and implementation of breeding and genetic resources conservation strategies.

In addition, study on the pattern of genetic variation in other associated species of ecological and economical importance would also provide useful information for developing proper and effective conservation strategies for the species complex.

2. Spatial distribution or fine-scale genetic structure within populations should be investigated. This will provide vital information for developing strategies for sampling within populations in order to avoid sampling of related individuals as well as to harbour as large genetic variation as possible.

3. The temporal pattern of mating system should be examined in the same population and possibly on the same parent trees between years. This information is vital to design seed collection protocols, and specifically to determine whether seed collection should be carried out only in the years with a large number of flowering individuals within populations so that a large amount of genetic variation would be captured by collecting seeds from only a few trees within the population.

4. The study of quantitative variation needs to be extended to include more test sites as well as more growth seasons in order to investigate the degree of genotype-by-environmental interaction. This knowledge is essential to guide the establishment of breeding and deployment zones and to develop proper strategies for genetic resources management and utilization in *P. macrocarpus*.

5. The relationship between water stress and morphological adaptation or plasticity, such as dry matter allocation between shoot and root, needs to be examined. Since *P. macrocarpus* is a deciduous species, water stress acclimation that occurs in leaves would be beneficial to seedlings only in the current growth season. However, morphological adaptation to water stress, such as an increase in root volume although at the expense of shoot growth, would provide a longer term benefit to seedling survival and establishment in the field.

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APPENDICES

Appendix 1 Populations and families of *P. macrocarpus* included in nursery trial.

Population	Family	t_m[a]	SWT[b] (mg)	Germination[c] (%)	Survival[d] (%)	Population	Family	t_m	SWT (mg)	Germination (%)	Survival (%)
1	1	0.91	57.0	55	100.00	4	64	0.98	62.3	41	87.50
1	2	0.92	36.0	55	100.00	4	65	0.93	53.3	83	75.00
1	3	0.99	45.4	47	87.50	4	66	0.98	69.0	45	87.50
1	4	0.99	49.5	52	100.00	4	68	0.99	62.4	52	81.25
1	5	0.99	53.1	79	93.75	4	69	0.99	50.3	30	93.75
1	6	0.99	45.7	41	93.75	4	70	0.96	56.2	65	93.75
1	7	0.98	46.3	72	93.75	4	71	0.93	64.2	36	81.25
1	8	0.85	49.0	45	93.75	5	72	0.96	45.2	87	93.75
1	9	0.98	56.5	88	100.00	5	73	0.91	48.7	70	93.75
1	10	0.98	50.1	77	75.00	5	74	0.96	65.2	88	93.75
1	11	0.96	42.3	58	100.00	5	75	0.94	66.9	76	75.00
1	12	0.97	55.5	52	100.00	5	76	0.98	61.9	81	100.00
1	13	0.98	63.9	36	100.00	5	77	0.90	51.2	81	93.75
1	14	0.99	43.0	83	100.00	5	78	0.90	50.8	65	100.00
1	15	0.88	57.9	76	100.00	5	79	0.88	60.7	69	100.00
2	16	0.94	61.2	68	93.75	5	80	0.81	67.6	76	93.75
2	17	0.83	80.2	88	100.00	5	81	0.97	73.4	83	93.75
2	18	0.92	82.3	68	100.00	5	82	0.94	59.9	62	100.00
2	19	0.82	74.5	54	93.75	5	83	0.91	78.0	88	93.75
2	20	0.82	86.2	73	100.00	5	86	0.91	66.9	91	100.00
2	21	0.96	62.5	63	93.75	5	87	0.91	59.9	81	93.75
2	23	0.86	52.4	37	100.00	5	88	0.92	63.3	87	100.00
2	24	0.86	74.0	34	100.00	5	89	0.92	53.4	77	100.00
2	25	0.96	59.2	44	93.75	5	90	0.97	59.9	86	87.50
2	26	0.87	55.8	55	100.00	5	91	0.97	52.6	84	100.00
2	27	0.85	70.0	76	100.00	5	92	0.89	72.0	86	100.00
2	28	0.67	50.4	62	93.75	5	93	0.96	58.1	86	87.50
2	29	0.89	61.9	69	100.00	5	95	0.95	72.7	94	93.75
2	30	0.88	45.8	83	93.75	5	96	0.83	65.3	81	87.50
3	32	0.93	74.5	63	100.00	6	97	0.97	66.3	41	93.75
3	33	0.89	53.0	48	100.00	6	99	0.88	44.7	33	93.75
3	34	0.97	68.0	52	81.25	6	102	0.81	60.3	34	100.00
3	35	0.97	75.8	65	93.75	6	104	0.89	61.4	55	100.00
3	36	0.98	67.2	52	93.75	6	106	0.91	44.4	33	93.75
3	37	0.89	56.3	69	93.75	6	107	0.94	65.0	52	87.50
3	38	0.87	51.3	62	87.50	6	108	0.96	45.1	33	100.00
3	39	0.97	61.2	83	100.00	6	110	0.94	60.6	84	93.75
3	40	0.96	76.4	83	100.00	6	111	0.94	60.6	34	100.00
3	42	0.93	54.5	69	93.75	6	112	0.91	53.7	33	93.75
3	43	0.93	62.4	62	75.00	6	114	0.98	51.8	45	100.00
3	44	0.98	70.8	69	100.00	6	115	0.98	59.7	48	93.75
3	45	0.96	63.3	83	100.00	6	116	0.96	54.0	62	93.75
4	48	0.98	55.5	30	100.00	6	117	0.89	49.8	30	100.00
4	50	0.96	51.4	33	93.75	6	119	0.91	58.4	69	100.00
4	51	0.98	63.4	31	87.50	6	120	0.99	55.0	55	100.00
4	52	0.96	61.6	32	93.75	6	122	0.96	45.8	41	100.00
4	53	0.98	56.2	44	100.00	6	124	0.98	57.6	48	100.00
4	54	0.99	53.7	69	87.50	6	126	0.99	56.6	31	87.50
4	55	0.96	52.1	34	93.75	6	131	0.98	63.2	48	93.75
4	56	0.92	84.8	62	100.00	6	132	0.95	53.1	41	100.00
4	57	0.99	86.4	55	87.50	6	133	0.95	58.8	41	100.00
4	58	0.94	81.4	45	100.00	6	135	0.95	59.8	69	93.75
4	59	0.92	64.4	62	100.00	6	136	0.97	50.6	38	100.00
4	60	0.95	57.2	55	100.00	6	137	0.93	43.5	40	87.50
4	61	0.98	74.7	69	100.00	6	138	0.94	54.0	41	100.00
4	63	0.95	54.8	48	93.75	6	139	0.96	40.2	41	100.00

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).
[b] SWT indicates mean seed weight for each family averaged from 80 seeds sown.
[c] Germination percentage for each family determined from 80 seeds sown.
[d] Survival percentage of seedlings after 30-week growing period based on 16 seedlings used for each family.

Appendix 2 Family means and standard deviations (SD) for 3-week seedling height growth (H3).[a]

Population	Family	t_m	H3 (cm)		Population	Family	t_m	H3 (cm)	
			Mean	SD				Mean	SD
1	1	0.91	4.1	0.80	4	64	0.98	3.9	0.53
1	2	0.92	3.2	0.46	4	65	0.93	4.4	0.35
1	3	0.99	3.8	0.79	4	66	0.98	4.6	0.60
1	4	0.99	4.5	0.67	4	68	0.99	4.5	0.63
1	5	0.99	4.2	0.70	4	69	0.99	3.7	0.71
1	6	0.99	3.7	0.93	4	70	0.96	4.4	0.72
1	7	0.98	4.2	0.54	4	71	0.93	4.5	0.88
1	8	0.85	4.2	0.79	5	72	0.96	4.2	0.87
1	9	0.98	4.9	0.60	5	73	0.91	4.4	0.67
1	10	0.98	3.9	0.81	5	74	0.96	5.4	0.59
1	11	0.96	4.4	1.00	5	75	0.94	4.3	0.80
1	12	0.97	3.9	0.70	5	76	0.98	4.5	0.79
1	13	0.98	4.1	0.83	5	77	0.90	4.0	0.64
1	14	0.99	4.2	0.38	5	78	0.90	4.8	0.55
1	15	0.88	4.8	0.47	5	79	0.88	4.4	0.77
2	16	0.94	3.6	0.50	5	80	0.81	5.1	0.54
2	17	0.83	5.3	0.51	5	81	0.97	5.4	0.50
2	18	0.92	4.4	0.75	5	82	0.94	5.0	0.45
2	19	0.82	5.5	0.85	5	83	0.91	5.5	0.56
2	20	0.82	5.0	1.10	5	86	0.91	5.4	1.08
2	21	0.96	4.0	0.91	5	87	0.91	5.3	0.51
2	23	0.86	4.0	0.59	5	88	0.92	4.5	0.58
2	24	0.86	4.6	0.95	5	89	0.92	4.2	0.46
2	25	0.96	4.4	1.14	5	90	0.97	4.7	0.36
2	26	0.87	4.2	0.72	5	91	0.97	4.5	0.40
2	27	0.85	5.2	1.01	5	92	0.89	5.2	0.96
2	28	0.67	3.7	0.57	5	93	0.96	4.8	0.36
2	29	0.89	4.3	0.73	5	95	0.95	5.1	0.53
2	30	0.88	4.0	0.66	5	96	0.83	4.7	0.94
3	32	0.93	4.7	0.73	6	97	0.97	3.5	0.61
3	33	0.89	3.5	0.93	6	99	0.88	3.6	0.56
3	34	0.97	4.5	0.53	6	102	0.81	3.8	0.61
3	35	0.97	4.2	0.96	6	104	0.89	4.2	0.51
3	36	0.98	4.4	0.45	6	106	0.91	3.5	0.98
3	37	0.89	3.9	0.70	6	107	0.94	4.2	0.45
3	38	0.87	4.0	0.54	6	108	0.96	4.2	0.62
3	39	0.97	4.4	0.83	6	110	0.94	4.4	0.67
3	40	0.96	4.3	0.69	6	111	0.94	4.4	0.51
3	42	0.93	3.9	0.84	6	112	0.91	3.6	0.51
3	43	0.93	4.2	1.08	6	114	0.98	4.4	0.53
3	44	0.98	5.1	0.58	6	115	0.98	5.1	0.69
3	45	0.96	4.8	0.92	6	116	0.96	4.4	0.72
4	48	0.98	4.4	0.72	6	117	0.89	4.0	0.79
4	50	0.96	4.1	0.62	6	119	0.91	4.2	0.72
4	51	0.98	4.4	0.45	6	120	0.99	3.8	0.60
4	52	0.96	4.4	0.91	6	122	0.96	3.7	0.47
4	53	0.98	3.8	0.60	6	124	0.98	4.2	0.55
4	54	0.99	4.1	0.62	6	126	0.99	3.5	0.51
4	55	0.96	4.0	0.84	6	131	0.98	4.2	0.68
4	56	0.92	5.3	1.05	6	132	0.95	3.0	0.58
4	57	0.99	4.9	0.59	6	133	0.95	4.0	0.80
4	58	0.94	5.4	1.07	6	135	0.95	4.1	0.46
4	59	0.92	5.1	0.51	6	136	0.97	3.8	0.52
4	60	0.95	4.2	0.91	6	137	0.93	3.5	0.81
4	61	0.98	4.9	0.48	6	138	0.94	3.7	0.66
4	63	0.95	4.2	0.77	6	139	0.96	3.3	0.75

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 3 Family means and standard deviations (SD) for 6-week seedling height growth (H6).[a]

Population	Family	t_m	H6 (cm)		Population	Family	t_m	H6 (cm)	
			Mean	SD				Mean	SD
1	1	0.91	8.0	2.13	4	64	0.98	6.8	1.19
1	2	0.92	6.4	1.76	4	65	0.93	7.1	0.79
1	3	0.99	7.6	1.22	4	66	0.98	7.4	0.67
1	4	0.99	7.4	1.32	4	68	0.99	7.0	1.10
1	5	0.99	6.2	0.64	4	69	0.99	7.0	1.63
1	6	0.99	6.2	1.21	4	70	0.96	6.9	0.99
1	7	0.98	6.8	0.71	4	71	0.93	7.7	1.18
1	8	0.85	6.4	1.30	5	72	0.96	6.6	1.64
1	9	0.98	7.0	1.06	5	73	0.91	7.6	1.12
1	10	0.98	6.3	0.98	5	74	0.96	9.7	1.18
1	11	0.96	7.6	2.27	5	75	0.94	7.8	1.38
1	12	0.97	6.1	0.91	5	76	0.98	7.8	1.38
1	13	0.98	6.3	0.73	5	77	0.90	6.5	1.04
1	14	0.99	6.1	0.70	5	78	0.90	6.8	1.03
1	15	0.88	7.2	0.63	5	79	0.88	6.9	1.29
2	16	0.94	5.5	0.70	5	80	0.81	7.7	0.97
2	17	0.83	8.1	1.24	5	81	0.97	9.1	1.15
2	18	0.92	7.3	0.94	5	82	0.94	7.5	1.13
2	19	0.82	7.8	1.13	5	83	0.91	9.6	1.43
2	20	0.82	7.9	0.75	5	86	0.91	8.1	0.87
2	21	0.96	6.7	1.74	5	87	0.91	8.0	1.25
2	23	0.86	6.6	1.46	5	88	0.92	7.1	0.96
2	24	0.86	8.0	1.56	5	89	0.92	6.4	0.69
2	25	0.96	7.2	0.83	5	90	0.97	6.6	0.77
2	26	0.87	6.6	0.89	5	91	0.97	7.1	0.91
2	27	0.85	8.3	1.21	5	92	0.89	8.7	1.45
2	28	0.67	6.1	1.05	5	93	0.96	7.0	1.14
2	29	0.89	7.0	1.06	5	95	0.95	8.5	0.99
2	30	0.88	5.2	0.58	5	96	0.83	8.0	1.50
3	32	0.93	7.2	1.27	6	97	0.97	6.7	0.93
3	33	0.89	6.7	1.48	6	99	0.88	5.1	0.97
3	34	0.97	6.8	0.68	6	102	0.81	7.5	2.12
3	35	0.97	7.3	0.81	6	104	0.89	5.7	0.85
3	36	0.98	6.5	0.86	6	106	0.91	6.7	2.17
3	37	0.89	5.7	0.77	6	107	0.94	7.5	1.24
3	38	0.87	5.8	0.80	6	108	0.96	7.1	2.22
3	39	0.97	7.1	1.24	6	110	0.94	6.4	1.17
3	40	0.96	7.0	0.99	6	111	0.94	7.2	1.28
3	42	0.93	7.2	1.04	6	112	0.91	7.0	2.13
3	43	0.93	6.9	1.64	6	114	0.98	5.7	0.72
3	44	0.98	7.9	0.86	6	115	0.98	6.6	0.82
3	45	0.96	8.8	1.33	6	116	0.96	6.5	0.91
4	48	0.98	6.8	0.95	6	117	0.89	7.4	1.53
4	50	0.96	7.0	1.34	6	119	0.91	6.6	0.83
4	51	0.98	8.6	1.81	6	120	0.99	5.8	0.95
4	52	0.96	8.0	1.36	6	122	0.96	5.4	0.75
4	53	0.98	6.1	1.05	6	124	0.98	6.7	0.90
4	54	0.99	6.4	0.99	6	126	0.99	5.2	0.92
4	55	0.96	6.6	0.96	6	131	0.98	6.4	0.82
4	56	0.92	8.5	1.57	6	132	0.95	6.5	2.00
4	57	0.99	7.4	1.22	6	133	0.95	6.2	0.94
4	58	0.94	9.1	1.69	6	135	0.95	5.5	0.54
4	59	0.92	7.6	0.78	6	136	0.97	6.1	1.32
4	60	0.95	6.8	1.09	6	137	0.93	6.6	1.59
4	61	0.98	8.6	1.38	6	138	0.94	7.3	2.15
4	63	0.95	6.5	1.07	6	139	0.96	5.0	0.54

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 4 Family means and standard deviations (SD) for 9-week seedling height growth (H9).[a]

Population	Family	t_m	H9 (cm) Mean	SD	Population	Family	t_m	H9 (cm) Mean	SD
1	1	0.91	11.1	2.51	4	64	0.98	10.5	1.23
1	2	0.92	9.3	1.86	4	65	0.93	10.4	1.12
1	3	0.99	11.1	2.37	4	66	0.98	10.8	1.50
1	4	0.99	11.0	1.62	4	68	0.99	11.5	1.94
1	5	0.99	9.3	1.22	4	69	0.99	10.5	1.83
1	6	0.99	9.4	1.91	4	70	0.96	11.4	1.36
1	7	0.98	11.1	1.85	4	71	0.93	12.3	1.88
1	8	0.85	10.4	2.49	5	72	0.96	10.9	1.41
1	9	0.98	11.3	1.76	5	73	0.91	12.1	1.70
1	10	0.98	10.8	1.36	5	74	0.96	15.7	1.70
1	11	0.96	10.0	2.20	5	75	0.94	13.7	2.10
1	12	0.97	8.9	1.62	5	76	0.98	14.8	2.13
1	13	0.98	9.4	1.69	5	77	0.90	10.3	1.93
1	14	0.99	8.4	1.08	5	78	0.90	10.8	1.22
1	15	0.88	11.4	1.53	5	79	0.88	11.6	2.04
2	16	0.94	9.9	1.32	5	80	0.81	12.7	1.83
2	17	0.83	13.0	1.95	5	81	0.97	14.3	1.77
2	18	0.92	11.9	1.46	5	82	0.94	14.2	1.59
2	19	0.82	13.1	2.46	5	83	0.91	14.9	2.02
2	20	0.82	13.5	1.62	5	86	0.91	14.3	1.95
2	21	0.96	10.8	1.68	5	87	0.91	14.1	1.84
2	23	0.86	11.5	1.75	5	88	0.92	11.1	1.82
2	24	0.86	12.5	1.77	5	89	0.92	10.7	0.83
2	25	0.96	11.9	1.58	5	90	0.97	11.8	1.70
2	26	0.87	9.5	1.26	5	91	0.97	13.2	2.16
2	27	0.85	13.3	1.95	5	92	0.89	14.9	2.07
2	28	0.67	10.3	1.37	5	93	0.96	12.4	2.07
2	29	0.89	12.6	1.29	5	95	0.95	15.5	2.24
2	30	0.88	10.1	1.17	5	96	0.83	14.5	2.06
3	32	0.93	11.7	1.98	6	97	0.97	11.2	1.93
3	33	0.89	10.4	1.82	6	99	0.88	8.1	1.50
3	34	0.97	11.7	1.26	6	102	0.81	12.0	2.14
3	35	0.97	12.3	1.95	6	104	0.89	10.0	1.58
3	36	0.98	11.6	1.42	6	106	0.91	10.4	2.29
3	37	0.89	9.2	1.45	6	107	0.94	12.8	1.86
3	38	0.87	8.9	0.95	6	108	0.96	11.2	2.43
3	39	0.97	10.9	1.88	6	110	0.94	12.1	1.59
3	40	0.96	13.1	1.81	6	111	0.94	13.0	1.70
3	42	0.93	12.5	1.83	6	112	0.91	11.0	2.31
3	43	0.93	11.6	2.82	6	114	0.98	10.8	1.65
3	44	0.98	13.3	1.94	6	115	0.98	10.6	1.70
3	45	0.96	14.7	1.64	6	116	0.96	11.6	1.41
4	48	0.98	10.2	1.81	6	117	0.89	11.6	1.60
4	50	0.96	11.3	1.58	6	119	0.91	12.6	1.83
4	51	0.98	14.2	2.02	6	120	0.99	10.0	1.41
4	52	0.96	11.2	1.45	6	122	0.96	10.6	1.29
4	53	0.98	9.8	1.99	6	124	0.98	12.7	2.08
4	54	0.99	9.9	1.15	6	126	0.99	9.1	1.53
4	55	0.96	9.8	1.58	6	131	0.98	11.4	1.46
4	56	0.92	13.4	2.02	6	132	0.95	11.1	1.06
4	57	0.99	11.6	2.06	6	133	0.95	12.1	1.64
4	58	0.94	13.4	2.22	6	135	0.95	10.2	1.15
4	59	0.92	11.4	1.03	6	136	0.97	10.7	1.79
4	60	0.95	10.1	1.60	6	137	0.93	10.3	1.66
4	61	0.98	13.9	1.39	6	138	0.94	12.1	2.36
4	63	0.95	11.8	2.34	6	139	0.96	8.7	1.14

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 5 Family means and standard deviations (SD) for 12-week seedling height growth (H12).[a]

Population	Family	t_m	H12 (cm) Mean	SD	Population	Family	t_m	H12 (cm) Mean	SD
1	1	0.91	16.6	4.19	4	64	0.98	18.0	2.20
1	2	0.92	14.9	2.94	4	65	0.93	18.0	2.86
1	3	0.99	16.8	2.93	4	66	0.98	17.9	2.73
1	4	0.99	18.6	3.20	4	68	0.99	19.0	4.46
1	5	0.99	14.5	2.41	4	69	0.99	16.7	2.32
1	6	0.99	15.3	2.76	4	70	0.96	19.6	2.39
1	7	0.98	18.2	1.97	4	71	0.93	20.9	3.11
1	8	0.85	17.4	3.71	5	72	0.96	17.8	1.66
1	9	0.98	18.1	3.04	5	73	0.91	21.5	2.31
1	10	0.98	17.1	2.59	5	74	0.96	25.8	1.94
1	11	0.96	14.0	3.10	5	75	0.94	22.0	3.09
1	12	0.97	14.8	2.71	5	76	0.98	23.7	3.35
1	13	0.98	16.2	3.27	5	77	0.90	17.5	2.29
1	14	0.99	16.0	3.37	5	78	0.90	19.2	2.36
1	15	0.88	19.4	1.69	5	79	0.88	20.5	2.19
2	16	0.94	16.3	2.68	5	80	0.81	20.9	2.41
2	17	0.83	21.3	2.91	5	81	0.97	25.4	2.39
2	18	0.92	18.7	3.16	5	82	0.94	21.9	3.38
2	19	0.82	20.3	3.42	5	83	0.91	26.5	3.20
2	20	0.82	20.8	2.56	5	86	0.91	23.1	2.57
2	21	0.96	16.4	3.06	5	87	0.91	23.8	3.68
2	23	0.86	19.2	3.64	5	88	0.92	17.9	2.64
2	24	0.86	21.8	4.26	5	89	0.92	18.0	3.25
2	25	0.96	20.6	3.30	5	90	0.97	19.7	2.17
2	26	0.87	15.0	1.89	5	91	0.97	22.4	2.41
2	27	0.85	22.6	3.69	5	92	0.89	24.7	3.53
2	28	0.67	16.5	2.54	5	93	0.96	20.1	2.47
2	29	0.89	18.9	2.84	5	95	0.95	26.2	2.41
2	30	0.88	15.7	2.30	5	96	0.83	23.0	3.61
3	32	0.93	18.8	4.14	6	97	0.97	19.3	3.50
3	33	0.89	15.5	2.16	6	99	0.88	15.5	2.88
3	34	0.97	18.5	2.63	6	102	0.81	19.0	2.44
3	35	0.97	18.3	3.17	6	104	0.89	17.2	4.34
3	36	0.98	19.0	2.90	6	106	0.91	16.1	2.89
3	37	0.89	14.5	3.49	6	107	0.94	22.5	3.68
3	38	0.87	15.4	2.70	6	108	0.96	16.9	2.53
3	39	0.97	16.5	3.29	6	110	0.94	20.3	2.78
3	40	0.96	22.7	2.67	6	111	0.94	21.5	3.10
3	42	0.93	19.5	2.93	6	112	0.91	16.9	3.01
3	43	0.93	18.0	3.32	6	114	0.98	18.9	3.14
3	44	0.98	21.9	2.97	6	115	0.98	18.5	2.68
3	45	0.96	23.6	2.69	6	116	0.96	19.3	3.53
4	48	0.98	17.6	3.66	6	117	0.89	18.1	3.23
4	50	0.96	18.8	2.67	6	119	0.91	20.4	2.80
4	51	0.98	23.0	3.45	6	120	0.99	17.4	2.51
4	52	0.96	18.9	3.17	6	122	0.96	17.2	3.15
4	53	0.98	17.7	4.16	6	124	0.98	20.0	2.22
4	54	0.99	16.5	1.98	6	126	0.99	15.6	4.10
4	55	0.96	17.8	4.73	6	131	0.98	18.2	2.37
4	56	0.92	21.5	3.64	6	132	0.95	17.1	3.31
4	57	0.99	19.3	3.27	6	133	0.95	19.9	1.67
4	58	0.94	22.1	3.55	6	135	0.95	17.5	2.13
4	59	0.92	18.8	2.00	6	136	0.97	17.8	2.71
4	60	0.95	17.1	2.96	6	137	0.93	14.9	2.33
4	61	0.98	23.1	2.19	6	138	0.94	18.6	2.65
4	63	0.95	19.3	4.28	6	139	0.96	14.9	2.61

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 6 Family means and standard deviations (SD) for 15-week seedling height growth (H15).[a]

Population	Family	t_m	H15 (cm) Mean	SD	Population	Family	t_m	H15 (cm) Mean	SD
1	1	0.91	18.4	5.57	4	64	0.98	22.4	2.95
1	2	0.92	18.0	4.51	4	65	0.93	22.0	4.39
1	3	0.99	18.9	3.55	4	66	0.98	20.9	3.46
1	4	0.99	23.1	4.41	4	68	0.99	23.1	7.38
1	5	0.99	16.7	4.05	4	69	0.99	21.6	4.11
1	6	0.99	17.6	4.38	4	70	0.96	23.8	3.95
1	7	0.98	22.4	4.33	4	71	0.93	23.6	3.64
1	8	0.85	18.4	4.39	5	72	0.96	19.9	2.41
1	9	0.98	19.8	3.37	5	73	0.91	24.3	2.71
1	10	0.98	19.6	4.11	5	74	0.96	29.5	4.08
1	11	0.96	16.5	3.34	5	75	0.94	26.3	5.30
1	12	0.97	17.5	2.75	5	76	0.98	27.4	5.51
1	13	0.98	19.5	4.59	5	77	0.90	20.1	2.81
1	14	0.99	19.2	5.62	5	78	0.90	21.3	2.58
1	15	0.88	22.0	3.28	5	79	0.88	23.4	2.79
2	16	0.94	19.6	4.77	5	80	0.81	24.6	4.27
2	17	0.83	24.2	4.16	5	81	0.97	27.5	3.50
2	18	0.92	23.7	3.76	5	82	0.94	25.6	4.19
2	19	0.82	24.0	5.54	5	83	0.91	30.6	3.35
2	20	0.82	26.2	5.59	5	86	0.91	27.3	4.66
2	21	0.96	18.4	3.91	5	87	0.91	26.6	5.06
2	23	0.86	22.9	4.46	5	88	0.92	20.7	3.79
2	24	0.86	24.2	4.48	5	89	0.92	21.0	2.62
2	25	0.96	24.0	4.63	5	90	0.97	22.0	2.79
2	26	0.87	18.8	3.15	5	91	0.97	24.9	3.17
2	27	0.85	27.2	4.64	5	92	0.89	28.7	4.39
2	28	0.67	19.5	3.16	5	93	0.96	22.6	3.00
2	29	0.89	21.5	3.22	5	95	0.95	29.9	2.36
2	30	0.88	18.8	2.56	5	96	0.83	27.3	5.67
3	32	0.93	21.5	4.73	6	97	0.97	23.8	5.09
3	33	0.89	18.9	4.20	6	99	0.88	20.3	4.18
3	34	0.97	19.9	2.92	6	102	0.81	22.8	3.75
3	35	0.97	19.8	3.75	6	104	0.89	21.0	5.02
3	36	0.98	22.9	5.16	6	106	0.91	19.8	6.10
3	37	0.89	19.3	6.26	6	107	0.94	24.7	4.26
3	38	0.87	18.9	3.32	6	108	0.96	21.5	5.03
3	39	0.97	19.1	4.47	6	110	0.94	24.3	6.00
3	40	0.96	28.0	5.12	6	111	0.94	25.1	4.07
3	42	0.93	23.4	3.39	6	112	0.91	20.6	6.27
3	43	0.93	20.8	3.71	6	114	0.98	23.0	5.32
3	44	0.98	26.3	4.50	6	115	0.98	22.8	3.26
3	45	0.96	29.9	4.66	6	116	0.96	22.6	5.32
4	48	0.98	23.0	5.08	6	117	0.89	20.5	4.19
4	50	0.96	23.2	4.53	6	119	0.91	21.8	4.43
4	51	0.98	29.6	7.29	6	120	0.99	19.3	3.98
4	52	0.96	24.3	5.38	6	122	0.96	20.3	5.27
4	53	0.98	20.5	6.13	6	124	0.98	23.2	3.92
4	54	0.99	20.6	3.45	6	126	0.99	18.1	5.16
4	55	0.96	20.6	6.09	6	131	0.98	20.6	3.90
4	56	0.92	25.7	4.04	6	132	0.95	19.6	3.86
4	57	0.99	23.2	4.40	6	133	0.95	23.3	3.60
4	58	0.94	27.5	4.99	6	135	0.95	20.6	4.31
4	59	0.92	21.4	2.32	6	136	0.97	20.5	4.51
4	60	0.95	22.7	4.52	6	137	0.93	17.3	3.18
4	61	0.98	26.5	3.86	6	138	0.94	22.3	3.99
4	63	0.95	23.4	6.89	6	139	0.96	18.0	3.82

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 7 Family means and standard deviations (SD) for 18-week seedling height growth (H18).[a]

Population	Family	t_m	H18 (cm) Mean	H18 (cm) SD	Population	Family	t_m	H18 (cm) Mean	H18 (cm) SD
1	1	0.91	23.2	7.90	4	64	0.98	27.6	6.99
1	2	0.92	22.7	7.90	4	65	0.93	28.7	8.62
1	3	0.99	26.8	8.62	4	66	0.98	27.2	6.39
1	4	0.99	31.1	8.74	4	68	0.99	28.1	10.30
1	5	0.99	19.9	6.42	4	69	0.99	29.9	5.26
1	6	0.99	24.9	7.00	4	70	0.96	33.0	7.34
1	7	0.98	28.4	6.50	4	71	0.93	28.9	7.28
1	8	0.85	24.6	6.35	5	72	0.96	26.4	6.14
1	9	0.98	25.2	6.37	5	73	0.91	31.6	5.26
1	10	0.98	24.6	4.70	5	74	0.96	38.7	6.95
1	11	0.96	20.9	4.92	5	75	0.94	30.7	7.91
1	12	0.97	22.6	6.04	5	76	0.98	36.7	9.36
1	13	0.98	24.5	7.57	5	77	0.90	26.6	6.88
1	14	0.99	24.7	8.50	5	78	0.90	27.8	5.81
1	15	0.88	28.4	5.58	5	79	0.88	33.0	6.79
2	16	0.94	23.0	6.50	5	80	0.81	29.3	6.55
2	17	0.83	28.8	7.28	5	81	0.97	32.2	5.98
2	18	0.92	28.8	7.76	5	82	0.94	30.9	7.01
2	19	0.82	28.2	6.56	5	83	0.91	39.9	6.71
2	20	0.82	33.2	10.00	5	86	0.91	37.8	6.99
2	21	0.96	24.8	7.82	5	87	0.91	32.5	7.36
2	23	0.86	28.2	7.58	5	88	0.92	26.6	6.36
2	24	0.86	30.3	6.36	5	89	0.92	27.7	7.25
2	25	0.96	31.7	6.86	5	90	0.97	26.5	6.40
2	26	0.87	23.4	5.69	5	91	0.97	32.0	6.75
2	27	0.85	33.7	6.72	5	92	0.89	36.0	6.18
2	28	0.67	24.4	5.61	5	93	0.96	29.7	5.36
2	29	0.89	27.4	7.67	5	95	0.95	35.8	5.50
2	30	0.88	26.2	7.36	5	96	0.83	34.6	8.59
3	32	0.93	26.8	9.38	6	97	0.97	30.5	7.63
3	33	0.89	24.0	8.63	6	99	0.88	30.3	10.44
3	34	0.97	25.5	7.06	6	102	0.81	32.9	7.29
3	35	0.97	26.1	7.73	6	104	0.89	26.8	7.63
3	36	0.98	30.3	8.80	6	106	0.91	26.3	9.45
3	37	0.89	26.8	7.38	6	107	0.94	30.4	6.06
3	38	0.87	24.7	7.62	6	108	0.96	29.1	7.65
3	39	0.97	24.1	8.10	6	110	0.94	29.4	8.28
3	40	0.96	36.0	6.72	6	111	0.94	31.5	6.88
3	42	0.93	35.1	10.14	6	112	0.91	27.3	9.94
3	43	0.93	24.7	7.06	6	114	0.98	29.9	7.29
3	44	0.98	35.5	9.89	6	115	0.98	29.7	5.60
3	45	0.96	37.7	7.30	6	116	0.96	32.6	7.05
4	48	0.98	29.6	7.97	6	117	0.89	26.6	6.61
4	50	0.96	34.1	5.99	6	119	0.91	25.4	7.70
4	51	0.98	38.8	10.12	6	120	0.99	23.0	6.47
4	52	0.96	32.6	9.24	6	122	0.96	28.0	9.63
4	53	0.98	30.4	11.18	6	124	0.98	29.3	4.72
4	54	0.99	29.7	5.24	6	126	0.99	22.4	5.35
4	55	0.96	24.7	7.62	6	131	0.98	25.3	6.98
4	56	0.92	31.6	6.85	6	132	0.95	26.4	6.39
4	57	0.99	31.3	8.18	6	133	0.95	31.9	7.73
4	58	0.94	37.4	5.77	6	135	0.95	27.3	7.97
4	59	0.92	28.6	6.21	6	136	0.97	26.0	6.74
4	60	0.95	31.0	7.66	6	137	0.93	20.5	4.31
4	61	0.98	33.9	8.54	6	138	0.94	28.7	6.70
4	63	0.95	29.8	10.06	6	139	0.96	22.0	6.48

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 8 Family means and standard deviations (SD) for 21-week seedling height growth (H21).[a]

Population	Family	t_m	H21 (cm)		Population	Family	t_m	H21 (cm)	
			Mean	SD				Mean	SD
1	1	0.91	25.9	9.45	4	64	0.98	29.5	8.87
1	2	0.92	25.6	8.50	4	65	0.93	32.1	9.72
1	3	0.99	31.1	9.83	4	66	0.98	31.3	7.42
1	4	0.99	35.2	7.92	4	68	0.99	29.9	10.99
1	5	0.99	23.3	9.18	4	69	0.99	33.3	6.43
1	6	0.99	29.5	8.52	4	70	0.96	36.2	7.53
1	7	0.98	29.3	6.60	4	71	0.93	30.8	7.72
1	8	0.85	25.8	6.65	5	72	0.96	28.2	7.19
1	9	0.98	29.3	11.64	5	73	0.91	36.3	6.54
1	10	0.98	27.0	6.51	5	74	0.96	41.5	5.52
1	11	0.96	26.4	6.37	5	75	0.94	35.9	8.50
1	12	0.97	25.3	7.20	5	76	0.98	39.2	9.72
1	13	0.98	27.4	8.08	5	77	0.90	30.4	8.84
1	14	0.99	28.1	8.53	5	78	0.90	32.3	6.90
1	15	0.88	28.7	6.25	5	79	0.88	38.7	8.84
2	16	0.94	23.8	6.14	5	80	0.81	32.7	6.63
2	17	0.83	31.0	7.79	5	81	0.97	36.0	8.58
2	18	0.92	29.3	7.22	5	82	0.94	37.7	8.72
2	19	0.82	29.5	7.65	5	83	0.91	46.5	7.93
2	20	0.82	35.4	10.04	5	86	0.91	40.5	7.58
2	21	0.96	26.5	8.20	5	87	0.91	35.6	6.48
2	23	0.86	31.2	7.86	5	88	0.92	28.9	6.99
2	24	0.86	33.7	4.79	5	89	0.92	32.3	6.71
2	25	0.96	33.0	5.89	5	90	0.97	30.8	8.50
2	26	0.87	24.8	5.44	5	91	0.97	37.2	8.14
2	27	0.85	35.5	8.65	5	92	0.89	40.6	7.11
2	28	0.67	24.5	5.38	5	93	0.96	32.2	6.31
2	29	0.89	27.6	7.32	5	95	0.95	39.6	5.82
2	30	0.88	28.7	6.92	5	96	0.83	38.6	9.87
3	32	0.93	30.0	10.06	6	97	0.97	33.7	9.94
3	33	0.89	27.4	9.31	6	99	0.88	33.8	9.76
3	34	0.97	31.8	9.81	6	102	0.81	36.4	6.42
3	35	0.97	30.7	10.22	6	104	0.89	30.2	10.31
3	36	0.98	33.3	9.09	6	106	0.91	30.4	11.22
3	37	0.89	28.5	7.89	6	107	0.94	35.8	9.92
3	38	0.87	27.1	8.76	6	108	0.96	31.2	6.86
3	39	0.97	26.6	8.83	6	110	0.94	32.8	10.67
3	40	0.96	38.4	8.40	6	111	0.94	36.6	6.76
3	42	0.93	41.7	8.26	6	112	0.91	32.2	11.52
3	43	0.93	29.4	11.25	6	114	0.98	33.8	9.24
3	44	0.98	38.9	10.89	6	115	0.98	34.0	6.42
3	45	0.96	39.3	7.58	6	116	0.96	34.3	7.63
4	48	0.98	33.3	7.10	6	117	0.89	28.6	6.25
4	50	0.96	37.9	8.14	6	119	0.91	28.3	9.55
4	51	0.98	41.9	11.99	6	120	0.99	26.5	7.49
4	52	0.96	37.5	12.34	6	122	0.96	31.0	9.48
4	53	0.98	34.9	10.55	6	124	0.98	33.8	8.31
4	54	0.99	30.8	5.72	6	126	0.99	26.5	7.15
4	55	0.96	28.7	8.85	6	131	0.98	29.1	8.34
4	56	0.92	33.8	7.69	6	132	0.95	30.9	7.48
4	57	0.99	33.4	8.54	6	133	0.95	35.3	7.79
4	58	0.94	38.5	6.02	6	135	0.95	29.5	8.40
4	59	0.92	33.0	7.16	6	136	0.97	28.3	7.95
4	60	0.95	36.5	7.47	6	137	0.93	22.7	5.44
4	61	0.98	39.5	9.97	6	138	0.94	31.5	7.33
4	63	0.95	34.3	12.74	6	139	0.96	24.7	7.19

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 9 Family means and standard deviations (SD) for 24-week seedling height growth (H24).[a]

Population	Family	t_m	H24 (cm) Mean	SD	Population	Family	t_m	H24 (cm) Mean	SD
1	1	0.91	27.1	9.15	4	64	0.98	31.4	8.32
1	2	0.92	26.1	8.41	4	65	0.93	32.6	10.34
1	3	0.99	31.7	9.40	4	66	0.98	31.6	7.46
1	4	0.99	35.5	8.06	4	68	0.99	32.6	9.90
1	5	0.99	24.9	8.49	4	69	0.99	33.9	6.61
1	6	0.99	29.9	8.44	4	70	0.96	36.7	7.65
1	7	0.98	29.9	6.26	4	71	0.93	32.0	7.92
1	8	0.85	26.4	6.18	5	72	0.96	30.3	7.44
1	9	0.98	29.9	11.89	5	73	0.91	38.2	5.81
1	10	0.98	27.9	6.72	5	74	0.96	42.5	5.09
1	11	0.96	28.1	7.61	5	75	0.94	38.8	7.45
1	12	0.97	25.8	7.16	5	76	0.98	40.5	9.15
1	13	0.98	28.4	7.98	5	77	0.90	31.5	8.31
1	14	0.99	28.7	8.66	5	78	0.90	33.5	7.27
1	15	0.88	29.4	6.05	5	79	0.88	40.4	7.67
2	16	0.94	23.9	6.26	5	80	0.81	33.0	6.54
2	17	0.83	30.8	7.76	5	81	0.97	36.4	8.48
2	18	0.92	29.5	7.12	5	82	0.94	39.6	7.76
2	19	0.82	29.8	7.53	5	83	0.91	47.3	7.77
2	20	0.82	36.0	9.93	5	86	0.91	41.6	6.65
2	21	0.96	27.2	7.85	5	87	0.91	36.1	6.28
2	23	0.86	32.6	7.93	5	88	0.92	30.2	6.75
2	24	0.86	34.4	5.14	5	89	0.92	33.2	5.95
2	25	0.96	34.3	5.33	5	90	0.97	31.9	8.87
2	26	0.87	25.1	5.42	5	91	0.97	38.4	7.79
2	27	0.85	36.0	8.63	5	92	0.89	41.3	7.04
2	28	0.67	25.1	5.16	5	93	0.96	32.9	6.45
2	29	0.89	28.4	7.03	5	95	0.95	40.7	5.30
2	30	0.88	28.8	7.11	5	96	0.83	39.8	9.70
3	32	0.93	30.9	9.78	6	97	0.97	35.3	9.98
3	33	0.89	28.3	9.44	6	99	0.88	34.2	9.89
3	34	0.97	35.0	9.50	6	102	0.81	37.1	6.18
3	35	0.97	31.3	10.10	6	104	0.89	31.2	10.33
3	36	0.98	34.3	8.85	6	106	0.91	31.2	11.82
3	37	0.89	30.2	7.68	6	107	0.94	36.6	10.03
3	38	0.87	28.1	9.07	6	108	0.96	32.3	6.63
3	39	0.97	27.9	8.73	6	110	0.94	35.1	11.65
3	40	0.96	39.0	8.01	6	111	0.94	39.0	7.35
3	42	0.93	42.3	7.95	6	112	0.91	33.2	11.75
3	43	0.93	30.6	10.74	6	114	0.98	34.6	9.03
3	44	0.98	39.5	11.06	6	115	0.98	34.7	6.37
3	45	0.96	40.1	7.75	6	116	0.96	36.0	6.78
4	48	0.98	33.6	7.29	6	117	0.89	29.8	5.87
4	50	0.96	38.4	8.00	6	119	0.91	29.7	9.06
4	51	0.98	45.2	9.60	6	120	0.99	27.5	8.65
4	52	0.96	40.3	11.09	6	122	0.96	32.1	9.25
4	53	0.98	35.9	10.98	6	124	0.98	35.0	7.85
4	54	0.99	31.5	5.52	6	126	0.99	27.1	7.54
4	55	0.96	29.1	9.01	6	131	0.98	29.7	8.18
4	56	0.92	34.2	7.89	6	132	0.95	31.6	7.64
4	57	0.99	35.4	6.13	6	133	0.95	36.3	7.76
4	58	0.94	38.9	6.09	6	135	0.95	30.2	8.34
4	59	0.92	33.4	6.93	6	136	0.97	28.9	7.54
4	60	0.95	37.1	7.67	6	137	0.93	24.2	4.92
4	61	0.98	40.0	9.65	6	138	0.94	32.1	7.10
4	63	0.95	35.6	13.06	6	139	0.96	26.0	7.29

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 10 Family means and standard deviations (SD) for 27-week seedling height growth (H27).[a]

Population	Family	t_m	H27 (cm)		Population	Family	t_m	H27 (cm)	
			Mean	SD				Mean	SD
1	1	0.91	27.7	9.19	4	64	0.98	31.8	8.08
1	2	0.92	26.3	8.49	4	65	0.93	33.2	10.62
1	3	0.99	32.5	9.51	4	66	0.98	32.9	6.67
1	4	0.99	35.7	8.13	4	68	0.99	33.3	9.61
1	5	0.99	25.1	8.61	4	69	0.99	36.2	8.50
1	6	0.99	30.6	8.45	4	70	0.96	37.6	7.89
1	7	0.98	30.4	6.18	4	71	0.93	33.1	7.51
1	8	0.85	26.8	5.95	5	72	0.96	32.9	9.38
1	9	0.98	30.7	11.66	5	73	0.91	41.9	8.83
1	10	0.98	28.6	6.54	5	74	0.96	45.9	9.58
1	11	0.96	31.8	8.70	5	75	0.94	40.1	8.78
1	12	0.97	26.0	7.38	5	76	0.98	43.5	11.73
1	13	0.98	28.8	7.83	5	77	0.90	35.4	11.84
1	14	0.99	29.0	8.75	5	78	0.90	37.2	10.83
1	15	0.88	29.6	6.08	5	79	0.88	47.8	12.58
2	16	0.94	24.3	6.16	5	80	0.81	34.0	6.72
2	17	0.83	31.5	9.16	5	81	0.97	38.1	10.09
2	18	0.92	30.1	7.17	5	82	0.94	42.1	14.51
2	19	0.82	30.6	7.21	5	83	0.91	50.9	10.59
2	20	0.82	37.9	11.15	5	86	0.91	45.8	10.52
2	21	0.96	27.4	7.67	5	87	0.91	36.6	6.40
2	23	0.86	33.9	7.83	5	88	0.92	31.2	8.67
2	24	0.86	35.0	4.95	5	89	0.92	35.5	6.24
2	25	0.96	37.1	8.02	5	90	0.97	35.0	10.35
2	26	0.87	25.8	7.13	5	91	0.97	40.5	8.64
2	27	0.85	37.4	9.28	5	92	0.89	44.4	9.15
2	28	0.67	25.5	5.15	5	93	0.96	33.1	6.38
2	29	0.89	28.5	7.05	5	95	0.95	44.5	7.88
2	30	0.88	29.5	7.57	5	96	0.83	41.9	10.83
3	32	0.93	32.1	9.85	6	97	0.97	40.8	14.17
3	33	0.89	28.5	9.34	6	99	0.88	37.1	11.39
3	34	0.97	35.5	9.78	6	102	0.81	44.5	10.73
3	35	0.97	32.0	10.26	6	104	0.89	34.3	11.40
3	36	0.98	34.8	8.78	6	106	0.91	35.3	18.24
3	37	0.89	31.8	8.57	6	107	0.94	39.1	10.77
3	38	0.87	29.8	10.15	6	108	0.96	36.6	10.39
3	39	0.97	28.4	8.68	6	110	0.94	38.8	14.83
3	40	0.96	40.9	8.89	6	111	0.94	43.7	9.55
3	42	0.93	43.2	8.13	6	112	0.91	38.4	14.35
3	43	0.93	32.4	11.55	6	114	0.98	36.8	10.65
3	44	0.98	39.6	11.02	6	115	0.98	37.1	5.52
3	45	0.96	40.7	8.64	6	116	0.96	40.5	8.38
4	48	0.98	34.2	6.80	6	117	0.89	31.6	6.34
4	50	0.96	39.6	8.20	6	119	0.91	30.6	8.73
4	51	0.98	46.1	10.02	6	120	0.99	31.1	12.73
4	52	0.96	43.0	13.60	6	122	0.96	35.5	12.08
4	53	0.98	36.4	11.44	6	124	0.98	36.9	8.51
4	54	0.99	31.6	5.51	6	126	0.99	29.6	10.33
4	55	0.96	29.5	9.50	6	131	0.98	32.2	9.62
4	56	0.92	34.8	7.75	6	132	0.95	34.0	9.10
4	57	0.99	36.9	6.87	6	133	0.95	39.8	11.35
4	58	0.94	39.9	6.89	6	135	0.95	30.8	8.54
4	59	0.92	34.0	6.75	6	136	0.97	30.5	7.08
4	60	0.95	39.9	9.10	6	137	0.93	25.4	5.89
4	61	0.98	40.5	9.54	6	138	0.94	34.2	6.92
4	63	0.95	36.7	13.71	6	139	0.96	28.7	10.54

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 11 Family means and standard deviations (SD) for 30-week seedling height growth (H30).[a]

Population	Family	t_m	H30 (cm) Mean	SD	Population	Family	t_m	H30 (cm) Mean	SD
1	1	0.91	28.1	9.17	4	64	0.98	32.0	8.02
1	2	0.92	26.4	8.52	4	65	0.93	37.7	12.50
1	3	0.99	33.3	10.97	4	66	0.98	33.2	6.62
1	4	0.99	35.8	8.19	4	68	0.99	33.5	9.73
1	5	0.99	26.1	8.47	4	69	0.99	36.8	9.47
1	6	0.99	32.1	9.41	4	70	0.96	38.2	8.25
1	7	0.98	30.6	6.23	4	71	0.93	34.7	8.08
1	8	0.85	27.2	5.93	5	72	0.96	36.1	11.26
1	9	0.98	30.5	11.71	5	73	0.91	43.2	9.04
1	10	0.98	28.9	6.26	5	74	0.96	48.4	11.30
1	11	0.96	33.3	10.77	5	75	0.94	41.3	10.59
1	12	0.97	26.5	8.52	5	76	0.98	46.0	12.57
1	13	0.98	29.0	7.79	5	77	0.90	37.5	12.99
1	14	0.99	29.9	10.02	5	78	0.90	39.3	12.82
1	15	0.88	29.7	6.15	5	79	0.88	51.5	14.44
2	16	0.94	24.4	6.09	5	80	0.81	36.5	9.52
2	17	0.83	32.5	11.04	5	81	0.97	40.2	12.93
2	18	0.92	30.3	7.11	5	82	0.94	44.0	15.53
2	19	0.82	30.4	7.23	5	83	0.91	51.9	10.77
2	20	0.82	38.4	12.12	5	86	0.91	48.5	13.02
2	21	0.96	27.6	7.42	5	87	0.91	37.9	7.11
2	23	0.86	35.1	8.86	5	88	0.92	31.9	9.14
2	24	0.86	35.2	5.16	5	89	0.92	37.5	8.06
2	25	0.96	38.0	9.55	5	90	0.97	37.6	11.50
2	26	0.87	26.4	5.59	5	91	0.97	41.7	10.32
2	27	0.85	38.2	8.98	5	92	0.89	46.0	10.56
2	28	0.67	26.6	5.83	5	93	0.96	33.6	6.71
2	29	0.89	28.6	6.94	5	95	0.95	46.4	9.50
2	30	0.88	31.4	9.41	5	96	0.83	44.4	13.23
3	32	0.93	32.6	10.43	6	97	0.97	42.9	14.35
3	33	0.89	28.7	9.20	6	99	0.88	38.3	11.71
3	34	0.97	36.1	10.12	6	102	0.81	47.5	13.70
3	35	0.97	33.0	10.53	6	104	0.89	37.9	16.27
3	36	0.98	35.4	9.10	6	106	0.91	36.4	19.00
3	37	0.89	32.2	8.91	6	107	0.94	42.9	16.40
3	38	0.87	30.9	11.14	6	108	0.96	38.9	12.96
3	39	0.97	28.9	8.45	6	110	0.94	43.1	15.89
3	40	0.96	43.8	12.67	6	111	0.94	47.4	10.22
3	42	0.93	45.8	8.77	6	112	0.91	40.6	15.96
3	43	0.93	33.4	13.44	6	114	0.98	37.5	10.89
3	44	0.98	39.8	11.33	6	115	0.98	40.8	7.91
3	45	0.96	40.7	8.66	6	116	0.96	41.9	9.22
4	48	0.98	34.5	6.93	6	117	0.89	33.1	7.68
4	50	0.96	40.4	9.10	6	119	0.91	31.5	9.06
4	51	0.98	47.3	11.14	6	120	0.99	31.4	12.87
4	52	0.96	44.3	12.32	6	122	0.96	37.0	13.15
4	53	0.98	36.6	11.37	6	124	0.98	39.3	11.26
4	54	0.99	31.8	5.47	6	126	0.99	31.6	13.64
4	55	0.96	29.5	9.50	6	131	0.98	32.6	9.92
4	56	0.92	35.6	8.01	6	132	0.95	36.5	11.95
4	57	0.99	37.4	6.92	6	133	0.95	42.2	12.98
4	58	0.94	40.2	7.11	6	135	0.95	31.1	8.43
4	59	0.92	34.3	6.61	6	136	0.97	31.0	7.39
4	60	0.95	41.7	11.43	6	137	0.93	25.8	6.87
4	61	0.98	41.4	8.91	6	138	0.94	35.5	6.62
4	63	0.95	38.7	14.60	6	139	0.96	29.3	10.76

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 12 Family means and standard deviations (SD) for 12-week seedling diameter growth (D12).[a]

Population	Family	t_m	D12 (mm)		Population	Family	t_m	D12 (mm)	
			Mean	SD				Mean	SD
1	1	0.91	2.86	0.65	4	64	0.98	3.19	0.50
1	2	0.92	2.98	0.69	4	65	0.93	2.96	0.55
1	3	0.99	2.77	0.48	4	66	0.98	3.15	0.41
1	4	0.99	3.18	0.47	4	68	0.99	3.18	0.58
1	5	0.99	3.18	0.70	4	69	0.99	2.85	0.37
1	6	0.99	3.02	0.59	4	70	0.96	3.38	0.35
1	7	0.98	3.35	0.58	4	71	0.93	3.59	0.40
1	8	0.85	3.13	0.48	5	72	0.96	2.99	0.30
1	9	0.98	3.36	0.56	5	73	0.91	3.29	0.48
1	10	0.98	3.43	0.54	5	74	0.96	3.93	0.47
1	11	0.96	2.94	0.59	5	75	0.94	3.67	0.53
1	12	0.97	2.95	0.50	5	76	0.98	3.78	0.48
1	13	0.98	3.20	0.56	5	77	0.90	3.33	0.58
1	14	0.99	2.87	0.43	5	78	0.90	3.07	0.46
1	15	0.88	3.67	0.49	5	79	0.88	3.48	0.41
2	16	0.94	3.24	0.43	5	80	0.81	3.48	0.51
2	17	0.83	3.74	0.47	5	81	0.97	3.63	0.41
2	18	0.92	3.56	0.42	5	82	0.94	3.35	0.47
2	19	0.82	3.44	0.44	5	83	0.91	3.61	0.47
2	20	0.82	3.91	0.55	5	86	0.91	3.50	0.52
2	21	0.96	3.22	0.41	5	87	0.91	3.59	0.67
2	23	0.86	3.55	0.39	5	88	0.92	3.26	0.50
2	24	0.86	3.58	0.50	5	89	0.92	3.28	0.41
2	25	0.96	3.34	0.48	5	90	0.97	3.46	0.50
2	26	0.87	2.69	0.30	5	91	0.97	3.16	0.38
2	27	0.85	3.44	0.45	5	92	0.89	3.69	0.41
2	28	0.67	3.21	0.32	5	93	0.96	3.54	0.43
2	29	0.89	3.69	0.47	5	95	0.95	3.89	0.41
2	30	0.88	2.98	0.44	5	96	0.83	3.67	0.68
3	32	0.93	3.44	0.55	6	97	0.97	3.41	0.67
3	33	0.89	3.30	0.45	6	99	0.88	2.97	0.64
3	34	0.97	3.52	0.48	6	102	0.81	3.26	0.54
3	35	0.97	3.40	0.62	6	104	0.89	3.33	0.57
3	36	0.98	3.26	0.4	6	106	0.91	2.94	0.51
3	37	0.89	3.03	0.42	6	107	0.94	3.76	0.72
3	38	0.87	2.63	0.47	6	108	0.96	3.09	0.49
3	39	0.97	3.26	0.49	6	110	0.94	3.54	0.46
3	40	0.96	3.41	0.55	6	111	0.94	3.66	0.56
3	42	0.93	3.24	0.52	6	112	0.91	3.59	0.49
3	43	0.93	3.25	0.31	6	114	0.98	3.34	0.56
3	44	0.98	3.61	0.39	6	115	0.98	3.17	0.56
3	45	0.96	3.55	0.48	6	116	0.96	3.64	0.40
4	48	0.98	3.03	0.61	6	117	0.89	2.99	0.50
4	50	0.96	3.38	0.50	6	119	0.91	3.30	0.55
4	51	0.98	3.85	0.61	6	120	0.99	2.85	0.35
4	52	0.96	3.45	0.44	6	122	0.96	2.98	0.52
4	53	0.98	3.30	0.52	6	124	0.98	3.40	0.56
4	54	0.99	3.05	0.31	6	126	0.99	3.06	0.47
4	55	0.96	3.26	0.54	6	131	0.98	3.30	0.33
4	56	0.92	3.48	0.55	6	132	0.95	3.06	0.42
4	57	0.99	3.31	0.51	6	133	0.95	3.64	0.44
4	58	0.94	3.35	0.42	6	135	0.95	3.09	0.62
4	59	0.92	3.18	0.43	6	136	0.97	3.05	0.49
4	60	0.95	3.24	0.53	6	137	0.93	2.92	0.37
4	61	0.98	3.65	0.54	6	138	0.94	3.41	0.47
4	63	0.95	3.58	0.70	6	139	0.96	2.94	0.45

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 13 Family means and standard deviations (SD) for 15-week seedling diameter growth (D15).[a]

Population	Family	t_m	D15 (mm)		Population	Family	t_m	D15 (mm)	
			Mean	SD				Mean	SD
1	1	0.91	4.04	0.90	4	64	0.98	4.48	1.05
1	2	0.92	3.80	0.78	4	65	0.93	4.11	0.93
1	3	0.99	3.90	0.74	4	66	0.98	4.51	0.95
1	4	0.99	4.36	0.63	4	68	0.99	4.27	0.91
1	5	0.99	4.11	0.82	4	69	0.99	3.77	0.52
1	6	0.99	4.28	0.77	4	70	0.96	4.69	0.68
1	7	0.98	4.59	0.81	4	71	0.93	4.65	0.60
1	8	0.85	4.30	0.51	5	72	0.96	4.26	0.41
1	9	0.98	4.70	0.99	5	73	0.91	4.63	0.58
1	10	0.98	4.45	0.79	5	74	0.96	5.65	0.70
1	11	0.96	3.85	0.72	5	75	0.94	5.14	0.89
1	12	0.97	4.13	0.70	5	76	0.98	5.07	0.76
1	13	0.98	4.47	0.86	5	77	0.90	4.54	0.72
1	14	0.99	4.03	0.67	5	78	0.90	4.39	0.58
1	15	0.88	5.13	0.61	5	79	0.88	4.80	0.49
2	16	0.94	4.35	0.69	5	80	0.81	4.79	0.72
2	17	0.83	5.27	0.65	5	81	0.97	5.13	0.96
2	18	0.92	4.76	0.64	5	82	0.94	4.77	0.94
2	19	0.82	4.46	0.67	5	83	0.91	5.04	0.61
2	20	0.82	5.56	0.82	5	86	0.91	5.26	0.59
2	21	0.96	4.02	0.61	5	87	0.91	5.07	0.70
2	23	0.86	4.51	0.69	5	88	0.92	4.54	0.54
2	24	0.86	4.98	0.86	5	89	0.92	4.63	0.58
2	25	0.96	4.72	0.70	5	90	0.97	4.43	0.63
2	26	0.87	3.73	0.74	5	91	0.97	4.52	0.47
2	27	0.85	4.88	0.80	5	92	0.89	5.30	0.43
2	28	0.67	4.09	0.51	5	93	0.96	4.66	0.67
2	29	0.89	4.68	0.61	5	95	0.95	5.55	0.60
2	30	0.88	4.16	0.44	5	96	0.83	4.92	0.81
3	32	0.93	4.68	0.95	6	97	0.97	5.05	0.95
3	33	0.89	4.29	0.46	6	99	0.88	4.27	0.88
3	34	0.97	4.72	1.04	6	102	0.81	4.59	0.68
3	35	0.97	4.36	1.00	6	104	0.89	4.61	0.99
3	36	0.98	4.44	0.70	6	106	0.91	3.93	0.51
3	37	0.89	4.14	0.64	6	107	0.94	5.19	0.97
3	38	0.87	3.73	0.69	6	108	0.96	4.59	0.73
3	39	0.97	4.25	0.51	6	110	0.94	4.94	0.71
3	40	0.96	5.15	0.68	6	111	0.94	5.24	0.66
3	42	0.93	4.69	0.56	6	112	0.91	5.17	1.00
3	43	0.93	4.28	0.72	6	114	0.98	4.70	0.68
3	44	0.98	4.90	0.71	6	115	0.98	4.25	0.70
3	45	0.96	5.08	0.71	6	116	0.96	4.80	0.67
4	48	0.98	4.62	1.09	6	117	0.89	4.37	0.70
4	50	0.96	4.67	0.92	6	119	0.91	4.72	0.70
4	51	0.98	5.12	0.67	6	120	0.99	3.85	0.60
4	52	0.96	4.66	0.94	6	122	0.96	4.15	0.62
4	53	0.98	4.57	0.70	6	124	0.98	4.88	0.64
4	54	0.99	4.17	0.60	6	126	0.99	4.18	0.51
4	55	0.96	4.20	0.65	6	131	0.98	4.51	0.70
4	56	0.92	4.81	0.88	6	132	0.95	4.41	0.51
4	57	0.99	4.96	0.83	6	133	0.95	5.10	0.79
4	58	0.94	4.86	0.94	6	135	0.95	4.42	0.77
4	59	0.92	4.65	0.52	6	136	0.97	4.22	0.48
4	60	0.95	4.45	0.62	6	137	0.93	4.15	0.51
4	61	0.98	5.09	0.99	6	138	0.94	4.46	0.63
4	63	0.95	4.80	0.96	6	139	0.96	3.88	0.75

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 14 Family means and standard deviations (SD) for 18-week seedling diameter growth (D18).[a]

Population	Family	t_m	D18 (mm) Mean	SD	Population	Family	t_m	D18 (mm) Mean	SD
1	1	0.91	5.11	1.16	4	64	0.98	5.64	1.35
1	2	0.92	4.89	0.70	4	65	0.93	5.23	1.17
1	3	0.99	4.89	0.91	4	66	0.98	5.72	1.13
1	4	0.99	5.13	0.83	4	68	0.99	5.42	1.27
1	5	0.99	5.06	0.96	4	69	0.99	4.79	0.74
1	6	0.99	5.21	0.87	4	70	0.96	5.80	1.01
1	7	0.98	5.25	0.72	4	71	0.93	5.90	0.98
1	8	0.85	5.34	0.92	5	72	0.96	5.10	0.77
1	9	0.98	5.93	1.08	5	73	0.91	5.51	0.58
1	10	0.98	5.53	0.83	5	74	0.96	6.97	1.32
1	11	0.96	4.83	0.87	5	75	0.94	6.03	1.17
1	12	0.97	5.13	0.93	5	76	0.98	5.96	1.02
1	13	0.98	5.51	1.42	5	77	0.90	5.21	0.82
1	14	0.99	5.18	0.91	5	78	0.90	5.18	0.75
1	15	0.88	6.09	0.71	5	79	0.88	5.74	0.65
2	16	0.94	5.33	0.94	5	80	0.81	5.57	0.93
2	17	0.83	6.66	0.81	5	81	0.97	6.18	1.33
2	18	0.92	6.10	0.66	5	82	0.94	6.17	0.99
2	19	0.82	5.60	1.07	5	83	0.91	6.42	0.76
2	20	0.82	6.83	1.14	5	86	0.91	6.21	0.74
2	21	0.96	5.16	0.93	5	87	0.91	6.27	1.08
2	23	0.86	5.57	0.85	5	88	0.92	5.69	0.65
2	24	0.86	6.13	0.97	5	89	0.92	5.88	0.79
2	25	0.96	5.80	0.69	5	90	0.97	5.48	0.80
2	26	0.87	4.73	1.02	5	91	0.97	5.87	0.72
2	27	0.85	6.29	1.14	5	92	0.89	6.40	0.72
2	28	0.67	4.87	0.78	5	93	0.96	5.60	0.78
2	29	0.89	5.70	0.97	5	95	0.95	6.96	0.67
2	30	0.88	5.19	0.65	5	96	0.83	6.16	1.12
3	32	0.93	5.95	1.19	6	97	0.97	6.32	1.01
3	33	0.89	5.27	0.71	6	99	0.88	5.27	0.88
3	34	0.97	6.10	1.37	6	102	0.81	5.44	0.98
3	35	0.97	5.54	1.25	6	104	0.89	5.71	1.06
3	36	0.98	5.64	0.96	6	106	0.91	4.84	0.78
3	37	0.89	5.01	0.84	6	107	0.94	6.49	1.18
3	38	0.87	4.68	0.95	6	108	0.96	5.64	0.66
3	39	0.97	5.18	0.60	6	110	0.94	6.02	0.83
3	40	0.96	6.51	0.81	6	111	0.94	6.14	0.75
3	42	0.93	5.67	0.77	6	112	0.91	5.93	1.05
3	43	0.93	5.20	0.99	6	114	0.98	5.68	0.75
3	44	0.98	6.01	0.75	6	115	0.98	5.16	0.90
3	45	0.96	6.53	0.84	6	116	0.96	5.68	0.87
4	48	0.98	5.86	1.20	6	117	0.89	5.58	0.97
4	50	0.96	5.92	9.40	6	119	0.91	5.90	0.75
4	51	0.98	6.34	1.04	6	120	0.99	4.87	0.75
4	52	0.96	6.11	1.23	6	122	0.96	4.95	1.04
4	53	0.98	5.71	0.70	6	124	0.98	5.63	0.73
4	54	0.99	5.43	1.12	6	126	0.99	5.15	0.74
4	55	0.96	5.25	0.95	6	131	0.98	5.45	0.66
4	56	0.92	6.23	0.91	6	132	0.95	5.06	0.80
4	57	0.99	5.94	0.88	6	133	0.95	6.00	0.73
4	58	0.94	5.89	1.10	6	135	0.95	5.38	1.00
4	59	0.92	5.87	0.64	6	136	0.97	5.12	0.62
4	60	0.95	5.37	0.69	6	137	0.93	4.83	0.70
4	61	0.98	6.24	1.16	6	138	0.94	5.35	0.75
4	63	0.95	5.80	1.23	6	139	0.96	4.73	0.77

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 15 Family means and standard deviations (SD) for 21-week seedling diameter growth (D21).[a]

Population	Family	t_m	D21 (mm)		Population	Family	t_m	D21 (mm)	
			Mean	SD				Mean	SD
1	1	0.91	6.35	1.41	4	64	0.98	7.00	1.76
1	2	0.92	5.99	0.99	4	65	0.93	6.31	1.43
1	3	0.99	6.16	0.89	4	66	0.98	7.07	1.30
1	4	0.99	6.21	0.99	4	68	0.99	7.05	1.95
1	5	0.99	5.87	1.00	4	69	0.99	6.03	1.19
1	6	0.99	6.22	0.90	4	70	0.96	7.01	1.27
1	7	0.98	6.51	1.14	4	71	0.93	7.30	0.93
1	8	0.85	6.59	1.14	5	72	0.96	6.18	0.71
1	9	0.98	7.16	1.46	5	73	0.91	6.57	0.83
1	10	0.98	6.99	1.20	5	74	0.96	8.65	1.56
1	11	0.96	5.86	0.94	5	75	0.94	8.03	1.20
1	12	0.97	6.08	1.38	5	76	0.98	7.14	1.02
1	13	0.98	6.67	1.32	5	77	0.90	6.24	1.03
1	14	0.99	6.61	0.85	5	78	0.90	6.22	1.07
1	15	0.88	7.81	1.07	5	79	0.88	6.56	0.65
2	16	0.94	6.62	1.30	5	80	0.81	6.90	1.25
2	17	0.83	8.14	0.71	5	81	0.97	7.72	1.71
2	18	0.92	7.87	1.10	5	82	0.94	7.21	1.19
2	19	0.82	6.99	1.23	5	83	0.91	7.44	0.82
2	20	0.82	8.73	1.83	5	86	0.91	7.21	0.76
2	21	0.96	6.46	1.51	5	87	0.91	7.86	1.30
2	23	0.86	6.86	1.12	5	88	0.92	6.95	1.27
2	24	0.86	7.80	1.57	5	89	0.92	6.96	0.99
2	25	0.96	7.26	0.98	5	90	0.97	6.58	1.16
2	26	0.87	5.89	1.44	5	91	0.97	6.92	0.72
2	27	0.85	7.46	0.97	5	92	0.89	7.34	0.96
2	28	0.67	5.89	1.26	5	93	0.96	6.51	0.94
2	29	0.89	6.59	0.87	5	95	0.95	8.09	0.74
2	30	0.88	6.32	1.27	5	96	0.83	7.08	1.56
3	32	0.93	7.14	1.43	6	97	0.97	7.99	1.16
3	33	0.89	6.59	1.33	6	99	0.88	6.40	0.54
3	34	0.97	6.96	1.73	6	102	0.81	6.71	1.02
3	35	0.97	6.41	1.11	6	104	0.89	7.20	1.27
3	36	0.98	6.99	1.06	6	106	0.91	6.23	1.28
3	37	0.89	5.97	1.17	6	107	0.94	7.50	1.29
3	38	0.87	5.91	1.15	6	108	0.96	6.86	0.76
3	39	0.97	6.07	0.90	6	110	0.94	7.31	0.89
3	40	0.96	8.09	1.28	6	111	0.94	7.47	0.95
3	42	0.93	7.13	1.20	6	112	0.91	7.31	1.22
3	43	0.93	6.20	1.06	6	114	0.98	7.09	1.09
3	44	0.98	7.53	1.53	6	115	0.98	6.45	0.76
3	45	0.96	8.40	1.79	6	116	0.96	7.26	1.27
4	48	0.98	7.12	1.45	6	117	0.89	6.56	0.91
4	50	0.96	7.54	1.00	6	119	0.91	6.75	0.93
4	51	0.98	7.88	1.63	6	120	0.99	5.71	0.72
4	52	0.96	7.78	1.50	6	122	0.96	5.83	1.05
4	53	0.98	7.17	1.20	6	124	0.98	6.71	0.69
4	54	0.99	6.81	1.36	6	126	0.99	6.04	0.85
4	55	0.96	6.46	1.35	6	131	0.98	6.28	0.67
4	56	0.92	7.89	1.12	6	132	0.95	6.15	1.04
4	57	0.99	7.15	1.38	6	133	0.95	7.32	0.65
4	58	0.94	7.31	1.08	6	135	0.95	6.23	0.91
4	59	0.92	7.20	0.73	6	136	0.97	6.01	0.78
4	60	0.95	6.57	1.05	6	137	0.93	6.24	0.83
4	61	0.98	7.75	1.14	6	138	0.94	7.05	1.03
4	63	0.95	7.24	1.43	6	139	0.96	5.75	0.87

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 16 Family means and standard deviations (SD) for 24-week seedling diameter growth (D24).[a]

Population	Family	t_m	D24 (mm)		Population	Family	t_m	D24 (mm)	
			Mean	SD				Mean	SD
1	1	0.91	7.34	1.53	4	64	0.98	8.76	2.18
1	2	0.92	7.53	1.31	4	65	0.93	7.70	1.76
1	3	0.99	7.40	0.90	4	66	0.98	8.44	1.67
1	4	0.99	7.46	1.07	4	68	0.99	8.91	2.37
1	5	0.99	6.96	1.50	4	69	0.99	7.24	1.44
1	6	0.99	7.43	1.20	4	70	0.96	8.43	1.64
1	7	0.98	8.02	1.34	4	71	0.93	9.02	1.46
1	8	0.85	7.99	1.52	5	72	0.96	7.84	1.08
1	9	0.98	8.23	1.68	5	73	0.91	8.00	0.95
1	10	0.98	8.18	1.42	5	74	0.96	10.72	1.63
1	11	0.96	7.54	1.52	5	75	0.94	9.82	1.38
1	12	0.97	7.48	1.31	5	76	0.98	8.66	1.29
1	13	0.98	7.73	1.80	5	77	0.90	7.89	1.47
1	14	0.99	7.84	1.21	5	78	0.90	7.62	1.40
1	15	0.88	9.18	1.46	5	79	0.88	8.20	1.02
2	16	0.94	7.69	1.35	5	80	0.81	8.45	1.58
2	17	0.83	9.19	0.98	5	81	0.97	9.33	1.87
2	18	0.92	8.94	1.18	5	82	0.94	9.02	1.55
2	19	0.82	8.07	1.77	5	83	0.91	8.80	1.03
2	20	0.82	10.08	2.06	5	86	0.91	8.97	1.00
2	21	0.96	7.86	1.79	5	87	0.91	9.59	1.47
2	23	0.86	8.05	1.07	5	88	0.92	8.11	1.47
2	24	0.86	9.24	1.74	5	89	0.92	8.44	1.29
2	25	0.96	8.69	0.96	5	90	0.97	7.77	1.49
2	26	0.87	6.81	1.41	5	91	0.97	8.45	0.79
2	27	0.85	8.61	0.97	5	92	0.89	8.58	1.12
2	28	0.67	7.14	1.43	5	93	0.96	8.10	1.69
2	29	0.89	7.82	1.22	5	95	0.95	9.80	1.28
2	30	0.88	7.65	1.37	5	96	0.83	8.83	1.98
3	32	0.93	8.17	1.67	6	97	0.97	9.56	1.51
3	33	0.89	7.68	1.53	6	99	0.88	7.86	1.12
3	34	0.97	8.52	1.62	6	102	0.81	8.48	1.18
3	35	0.97	7.53	1.56	6	104	0.89	8.41	1.37
3	36	0.98	8.13	1.11	6	106	0.91	7.60	1.34
3	37	0.89	7.27	1.23	6	107	0.94	9.38	1.45
3	38	0.87	7.20	1.28	6	108	0.96	8.51	1.14
3	39	0.97	7.22	1.05	6	110	0.94	9.09	1.54
3	40	0.96	9.64	1.32	6	111	0.94	9.13	0.86
3	42	0.93	8.54	0.94	6	112	0.91	8.70	1.43
3	43	0.93	7.12	0.95	6	114	0.98	8.75	1.54
3	44	0.98	8.89	1.71	6	115	0.98	8.05	1.50
3	45	0.96	9.41	1.85	6	116	0.96	9.16	1.04
4	48	0.98	8.34	1.66	6	117	0.89	7.93	1.31
4	50	0.96	8.92	1.07	6	119	0.91	8.23	1.26
4	51	0.98	9.99	1.47	6	120	0.99	7.45	1.00
4	52	0.96	9.27	1.95	6	122	0.96	7.20	1.14
4	53	0.98	8.38	1.49	6	124	0.98	8.11	0.86
4	54	0.99	8.05	1.42	6	126	0.99	7.28	1.01
4	55	0.96	7.88	1.54	6	131	0.98	7.64	0.80
4	56	0.92	9.05	1.20	6	132	0.95	7.60	1.43
4	57	0.99	9.04	1.40	6	133	0.95	9.36	1.14
4	58	0.94	8.72	1.26	6	135	0.95	7.85	2.11
4	59	0.92	8.57	0.91	6	136	0.97	7.21	1.03
4	60	0.95	7.90	1.12	6	137	0.93	7.36	1.32
4	61	0.98	9.01	1.24	6	138	0.94	8.51	1.27
4	63	0.95	8.90	1.83	6	139	0.96	7.32	0.98

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 17 Family means and standard deviations (SD) for 27-week seedling diameter growth (D27).[a]

Population	Family	t_m	D27 (mm) Mean	SD	Population	Family	t_m	D27 (mm) Mean	SD
1	1	0.91	8.56	1.76	4	64	0.98	10.14	2.94
1	2	0.92	8.86	1.60	4	65	0.93	8.88	2.14
1	3	0.99	8.78	1.17	4	66	0.98	9.92	1.65
1	4	0.99	8.08	1.26	4	68	0.99	9.75	2.32
1	5	0.99	8.09	1.77	4	69	0.99	8.49	2.12
1	6	0.99	8.71	1.60	4	70	0.96	9.89	1.82
1	7	0.98	8.70	1.49	4	71	0.93	9.99	1.73
1	8	0.85	8.85	1.68	5	72	0.96	8.78	1.27
1	9	0.98	9.48	2.14	5	73	0.91	9.29	1.09
1	10	0.98	9.48	1.58	5	74	0.96	12.46	1.79
1	11	0.96	8.86	1.68	5	75	0.94	11.36	1.68
1	12	0.97	8.55	1.85	5	76	0.98	10.24	1.51
1	13	0.98	9.09	2.03	5	77	0.90	9.12	1.85
1	14	0.99	9.15	1.58	5	78	0.90	9.05	1.93
1	15	0.88	10.21	1.34	5	79	0.88	10.06	1.77
2	16	0.94	8.34	1.49	5	80	0.81	9.54	1.98
2	17	0.83	10.25	1.61	5	81	0.97	10.72	2.23
2	18	0.92	9.92	1.48	5	82	0.94	10.09	1.84
2	19	0.82	9.11	2.15	5	83	0.91	10.57	1.44
2	20	0.82	11.51	2.49	5	86	0.91	10.45	1.54
2	21	0.96	9.05	1.82	5	87	0.91	11.04	1.73
2	23	0.86	9.00	1.38	5	88	0.92	9.27	1.69
2	24	0.86	9.99	1.93	5	89	0.92	9.96	1.44
2	25	0.96	9.65	1.04	5	90	0.97	9.11	1.83
2	26	0.87	7.29	1.61	5	91	0.97	9.81	1.15
2	27	0.85	9.79	1.32	5	92	0.89	10.15	1.29
2	28	0.67	8.00	1.22	5	93	0.96	9.55	1.88
2	29	0.89	8.59	1.30	5	95	0.95	11.69	1.71
2	30	0.88	8.71	1.71	5	96	0.83	10.54	2.02
3	32	0.93	9.30	1.93	6	97	0.97	11.06	2.05
3	33	0.89	8.64	1.57	6	99	0.88	9.35	1.35
3	34	0.97	9.48	1.72	6	102	0.81	9.82	1.55
3	35	0.97	8.29	1.49	6	104	0.89	9.42	1.64
3	36	0.98	9.36	1.46	6	106	0.91	8.87	1.86
3	37	0.89	8.24	1.57	6	107	0.94	10.77	1.76
3	38	0.87	8.33	1.46	6	108	0.96	9.47	1.24
3	39	0.97	7.99	1.08	6	110	0.94	10.46	2.06
3	40	0.96	10.60	1.34	6	111	0.94	10.74	1.48
3	42	0.93	9.78	1.17	6	112	0.91	9.90	1.95
3	43	0.93	8.06	1.53	6	114	0.98	10.20	1.86
3	44	0.98	9.91	1.98	6	115	0.98	9.39	1.66
3	45	0.96	11.11	2.12	6	116	0.96	10.50	1.50
4	48	0.98	9.69	1.76	6	117	0.89	9.18	1.53
4	50	0.96	10.03	1.33	6	119	0.91	9.58	1.71
4	51	0.98	11.75	1.73	6	120	0.99	8.41	0.70
4	52	0.96	10.83	2.38	6	122	0.96	8.42	1.51
4	53	0.98	9.70	1.99	6	124	0.98	9.33	1.04
4	54	0.99	9.01	1.70	6	126	0.99	8.79	1.55
4	55	0.96	9.26	1.91	6	131	0.98	8.69	0.81
4	56	0.92	10.23	1.60	6	132	0.95	9.00	1.68
4	57	0.99	10.49	1.58	6	133	0.95	10.83	1.18
4	58	0.94	10.20	1.68	6	135	0.95	9.31	2.20
4	59	0.92	10.14	1.40	6	136	0.97	8.43	1.54
4	60	0.95	8.99	1.44	6	137	0.93	8.63	1.45
4	61	0.98	10.70	1.21	6	138	0.94	9.65	1.66
4	63	0.95	10.40	2.31	6	139	0.96	8.42	1.21

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 18 Family means and standard deviations (SD) for 30-week seedling diameter growth (D30).[a]

Population	Family	t_m	D30 (mm)		Population	Family	t_m	D30 (mm)	
			Mean	SD				Mean	SD
1	1	0.91	9.93	2.04	4	64	0.98	10.98	2.99
1	2	0.92	9.96	2.13	4	65	0.93	9.86	2.55
1	3	0.99	9.64	1.40	4	66	0.98	10.80	1.84
1	4	0.99	9.03	1.77	4	68	0.99	10.32	2.28
1	5	0.99	9.08	1.87	4	69	0.99	9.17	2.02
1	6	0.99	9.27	1.54	4	70	0.96	11.03	2.00
1	7	0.98	9.05	1.44	4	71	0.93	11.15	2.07
1	8	0.85	9.47	1.72	5	72	0.96	9.81	1.18
1	9	0.98	10.61	2.41	5	73	0.91	10.18	1.03
1	10	0.98	10.34	1.76	5	74	0.96	13.44	1.48
1	11	0.96	9.59	1.63	5	75	0.94	12.26	1.44
1	12	0.97	9.27	2.14	5	76	0.98	10.92	1.64
1	13	0.98	9.99	2.18	5	77	0.90	9.99	1.91
1	14	0.99	9.91	1.82	5	78	0.90	9.73	1.98
1	15	0.88	11.24	1.42	5	79	0.88	10.85	1.64
2	16	0.94	8.97	1.61	5	80	0.81	10.51	2.19
2	17	0.83	10.88	1.61	5	81	0.97	11.89	2.25
2	18	0.92	10.45	1.71	5	82	0.94	11.11	2.10
2	19	0.82	9.89	2.06	5	83	0.91	11.98	1.09
2	20	0.82	12.49	2.48	5	86	0.91	11.31	1.52
2	21	0.96	9.93	2.15	5	87	0.91	12.41	1.39
2	23	0.86	9.48	1.30	5	88	0.92	9.96	1.68
2	24	0.86	10.76	1.72	5	89	0.92	10.76	1.53
2	25	0.96	10.20	1.30	5	90	0.97	9.98	1.99
2	26	0.87	7.96	1.82	5	91	0.97	10.60	1.30
2	27	0.85	10.59	1.41	5	92	0.89	11.03	1.53
2	28	0.67	9.03	1.65	5	93	0.96	10.55	1.88
2	29	0.89	9.16	1.44	5	95	0.95	12.56	1.57
2	30	0.88	9.21	1.83	5	96	0.83	11.43	2.14
3	32	0.93	10.12	2.08	6	97	0.97	11.73	1.94
3	33	0.89	9.48	1.67	6	99	0.88	10.06	1.50
3	34	0.97	10.04	1.97	6	102	0.81	10.68	1.51
3	35	0.97	9.17	1.70	6	104	0.89	10.31	1.99
3	36	0.98	10.20	1.55	6	106	0.91	9.63	2.06
3	37	0.89	8.92	2.03	6	107	0.94	11.65	2.12
3	38	0.87	9.14	1.53	6	108	0.96	10.07	1.06
3	39	0.97	8.93	1.36	6	110	0.94	11.59	1.91
3	40	0.96	11.21	1.47	6	111	0.94	11.59	1.62
3	42	0.93	10.74	1.32	6	112	0.91	10.66	2.23
3	43	0.93	8.44	1.58	6	114	0.98	11.07	1.76
3	44	0.98	11.01	2.13	6	115	0.98	10.43	2.03
3	45	0.96	12.03	2.33	6	116	0.96	11.46	1.44
4	48	0.98	10.50	2.14	6	117	0.89	9.91	1.66
4	50	0.96	10.71	1.39	6	119	0.91	10.52	1.94
4	51	0.98	12.98	2.09	6	120	0.99	8.97	0.89
4	52	0.96	11.75	2.77	6	122	0.96	9.15	1.41
4	53	0.98	10.49	2.05	6	124	0.98	10.14	1.09
4	54	0.99	9.69	1.72	6	126	0.99	9.54	1.72
4	55	0.96	9.96	1.79	6	131	0.98	9.48	1.15
4	56	0.92	11.28	2.15	6	132	0.95	9.86	1.98
4	57	0.99	11.10	1.56	6	133	0.95	11.46	1.15
4	58	0.94	11.16	1.99	6	135	0.95	9.97	2.28
4	59	0.92	10.93	1.47	6	136	0.97	9.23	1.38
4	60	0.95	9.76	1.53	6	137	0.93	9.08	1.55
4	61	0.98	11.74	1.38	6	138	0.94	10.61	1.76
4	63	0.95	11.28	2.78	6	139	0.96	9.04	1.32

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 19 Family means and standard deviations (SD) for leaf dry weight (LEAF).[a]

Population	Family	t_m	LEAF (g)		Population	Family	t_m	LEAF (g)	
			Mean	SD				Mean	SD
1	1	0.91	2.061	1.111	4	64	0.98	2.700	1.318
1	2	0.92	2.151	1.072	4	65	0.93	2.675	1.875
1	3	0.99	2.201	0.852	4	66	0.98	3.045	1.113
1	4	0.99	2.255	1.191	4	68	0.99	2.563	1.332
1	5	0.99	1.596	0.951	4	69	0.99	2.858	1.696
1	6	0.99	2.362	1.121	4	70	0.96	2.794	1.222
1	7	0.98	1.939	0.877	4	71	0.93	3.467	1.771
1	8	0.85	2.328	1.418	5	72	0.96	2.937	1.306
1	9	0.98	1.713	1.273	5	73	0.91	4.267	1.354
1	10	0.98	1.912	1.073	5	74	0.96	4.528	1.573
1	11	0.96	2.113	1.307	5	75	0.94	4.136	2.289
1	12	0.97	1.812	0.766	5	76	0.98	4.615	2.033
1	13	0.98	2.373	0.959	5	77	0.90	3.693	1.939
1	14	0.99	2.057	1.595	5	78	0.90	3.583	2.469
1	15	0.88	2.256	1.094	5	79	0.88	5.186	2.523
2	16	0.94	1.642	0.564	5	80	0.81	3.481	2.149
2	17	0.83	2.399	1.329	5	81	0.97	3.856	2.209
2	18	0.92	2.337	0.629	5	82	0.94	3.195	2.477
2	19	0.82	1.953	0.999	5	83	0.91	5.763	1.867
2	20	0.82	4.134	2.192	5	86	0.91	5.644	2.324
2	21	0.96	2.083	1.219	5	87	0.91	3.645	1.266
2	23	0.86	1.786	0.780	5	88	0.92	3.097	1.569
2	24	0.86	2.054	0.890	5	89	0.92	3.343	1.638
2	25	0.96	3.037	1.387	5	90	0.97	3.375	1.573
2	26	0.87	2.006	1.029	5	91	0.97	4.042	1.725
2	27	0.85	2.808	0.969	5	92	0.89	4.910	2.386
2	28	0.67	1.997	0.814	5	93	0.96	2.883	1.357
2	29	0.89	1.418	0.774	5	95	0.95	4.268	1.622
2	30	0.88	2.598	1.370	5	96	0.83	4.455	1.705
3	32	0.93	2.334	1.141	6	97	0.97	3.903	1.999
3	33	0.89	2.472	1.523	6	99	0.88	2.912	1.765
3	34	0.97	2.764	1.345	6	102	0.81	3.906	1.575
3	35	0.97	2.327	1.275	6	104	0.89	3.510	2.029
3	36	0.98	2.598	1.120	6	106	0.91	3.287	2.611
3	37	0.89	2.529	1.094	6	107	0.94	3.693	1.617
3	38	0.87	2.439	1.115	6	108	0.96	3.336	1.421
3	39	0.97	1.567	0.935	6	110	0.94	4.426	2.636
3	40	0.96	3.572	1.807	6	111	0.94	3.848	1.767
3	42	0.93	3.207	1.012	6	112	0.91	4.906	2.432
3	43	0.93	2.226	1.439	6	114	0.98	2.821	1.122
3	44	0.98	3.432	1.847	6	115	0.98	2.775	1.099
3	45	0.96	3.024	1.511	6	116	0.96	3.780	1.366
4	48	0.98	2.998	1.055	6	117	0.89	2.932	1.302
4	50	0.96	2.969	1.213	6	119	0.91	2.112	0.779
4	51	0.98	4.088	1.357	6	120	0.99	2.938	1.951
4	52	0.96	5.344	2.419	6	122	0.96	2.827	2.066
4	53	0.98	2.721	1.287	6	124	0.98	2.809	1.325
4	54	0.99	2.649	1.078	6	126	0.99	2.711	1.390
4	55	0.96	2.197	1.246	6	131	0.98	2.638	1.269
4	56	0.92	2.741	1.361	6	132	0.95	3.370	1.324
4	57	0.99	4.015	1.610	6	133	0.95	3.457	1.461
4	58	0.94	3.777	1.654	6	135	0.95	2.579	0.787
4	59	0.92	2.710	0.718	6	136	0.97	2.058	1.056
4	60	0.95	3.739	1.721	6	137	0.93	2.271	0.959
4	61	0.98	3.971	1.235	6	138	0.94	3.212	1.054
4	63	0.95	2.784	1.651	6	139	0.96	2.477	1.195

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 20 Family means and standard deviations (SD) for stem dry weight (STEM).[a]

Population	Family	t_m	STEM (g)		Population	Family	t_m	STEM (g)	
			Mean	SD				Mean	SD
1	1	0.91	2.426	1.429	4	64	0.98	3.166	2.077
1	2	0.92	1.974	0.803	4	65	0.93	3.242	2.041
1	3	0.99	2.585	1.112	4	66	0.98	3.695	1.580
1	4	0.99	2.748	1.058	4	68	0.99	3.358	2.525
1	5	0.99	1.710	0.888	4	69	0.99	3.196	1.884
1	6	0.99	2.311	1.134	4	70	0.96	3.368	1.426
1	7	0.98	2.389	1.281	4	71	0.93	3.305	1.697
1	8	0.85	2.436	1.319	5	72	0.96	2.493	0.892
1	9	0.98	2.410	1.597	5	73	0.91	3.756	1.177
1	10	0.98	2.335	1.293	5	74	0.96	6.551	1.487
1	11	0.96	2.181	0.861	5	75	0.94	4.885	2.208
1	12	0.97	2.136	1.171	5	76	0.98	4.520	1.866
1	13	0.98	2.586	1.570	5	77	0.90	2.808	1.307
1	14	0.99	2.342	1.236	5	78	0.90	3.214	2.032
1	15	0.88	2.878	1.304	5	79	0.88	4.752	2.683
2	16	0.94	1.670	0.726	5	80	0.81	3.461	2.188
2	17	0.83	3.224	1.339	5	81	0.97	4.053	2.561
2	18	0.92	2.896	1.132	5	82	0.94	3.595	2.226
2	19	0.82	2.808	1.549	5	83	0.91	5.471	1.394
2	20	0.82	5.285	2.379	5	86	0.91	5.499	1.832
2	21	0.96	2.142	1.206	5	87	0.91	4.818	2.251
2	23	0.86	2.262	0.758	5	88	0.92	2.409	1.379
2	24	0.86	2.831	0.985	5	89	0.92	3.132	1.221
2	25	0.96	3.581	0.957	5	90	0.97	3.008	1.433
2	26	0.87	1.802	0.911	5	91	0.97	4.218	1.683
2	27	0.85	3.546	1.380	5	92	0.89	4.768	1.834
2	28	0.67	1.973	0.719	5	93	0.96	3.114	1.210
2	29	0.89	1.991	0.698	5	95	0.95	5.492	1.837
2	30	0.88	2.370	0.862	5	96	0.83	4.842	2.319
3	32	0.93	2.931	1.352	6	97	0.97	4.034	2.706
3	33	0.89	2.194	1.103	6	99	0.88	2.953	1.658
3	34	0.97	3.002	1.500	6	102	0.81	3.612	1.550
3	35	0.97	2.350	0.961	6	104	0.89	3.201	1.641
3	36	0.98	3.462	1.630	6	106	0.91	2.806	2.439
3	37	0.89	2.436	1.179	6	107	0.94	4.384	2.591
3	38	0.87	2.503	1.771	6	108	0.96	3.036	1.064
3	39	0.97	1.968	1.054	6	110	0.94	4.487	4.490
3	40	0.96	3.912	1.599	6	111	0.94	3.849	1.655
3	42	0.93	3.581	1.229	6	112	0.91	4.335	2.707
3	43	0.93	1.979	1.462	6	114	0.98	3.536	1.436
3	44	0.98	3.214	1.625	6	115	0.98	2.909	1.332
3	45	0.96	4.202	2.057	6	116	0.96	4.049	1.633
4	48	0.98	3.191	1.524	6	117	0.89	2.984	1.346
4	50	0.96	3.673	1.334	6	119	0.91	2.592	1.262
4	51	0.98	5.922	2.640	6	120	0.99	2.015	1.611
4	52	0.96	5.656	2.891	6	122	0.96	2.704	1.578
4	53	0.98	3.805	2.369	6	124	0.98	2.932	1.325
4	54	0.99	2.946	1.294	6	126	0.99	2.225	1.280
4	55	0.96	2.601	1.943	6	131	0.98	2.439	1.045
4	56	0.92	3.688	2.030	6	132	0.95	2.504	1.053
4	57	0.99	4.554	1.894	6	133	0.95	3.701	1.496
4	58	0.94	4.575	2.399	6	135	0.95	2.219	1.080
4	59	0.92	3.358	1.285	6	136	0.97	2.097	1.136
4	60	0.95	3.801	2.024	6	137	0.93	1.794	0.917
4	61	0.98	5.007	2.184	6	138	0.94	3.237	1.359
4	63	0.95	3.799	2.615	6	139	0.96	1.823	1.098

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 21 Family means and standard deviations (SD) for tap root dry weight (TROOT).[a]

Population	Family	t_m	TROOT (g) Mean	SD	Population	Family	t_m	TROOT (g) Mean	SD
1	1	0.91	2.717	1.792	4	64	0.98	2.646	1.667
1	2	0.92	2.771	2.147	4	65	0.93	3.073	2.101
1	3	0.99	2.995	1.439	4	66	0.98	2.969	1.535
1	4	0.99	4.131	2.192	4	68	0.99	2.423	1.951
1	5	0.99	2.242	1.280	4	69	0.99	2.951	1.919
1	6	0.99	4.119	1.149	4	70	0.96	3.901	3.332
1	7	0.98	4.037	2.295	4	71	0.93	2.537	1.708
1	8	0.85	3.884	2.188	5	72	0.96	3.155	1.770
1	9	0.98	2.948	1.859	5	73	0.91	4.628	1.306
1	10	0.98	2.837	1.580	5	74	0.96	5.567	2.532
1	11	0.96	1.675	0.816	5	75	0.94	5.445	2.896
1	12	0.97	3.377	2.013	5	76	0.98	5.560	2.745
1	13	0.98	3.692	2.225	5	77	0.90	4.291	2.190
1	14	0.99	2.771	1.175	5	78	0.90	4.857	2.535
1	15	0.88	3.785	1.695	5	79	0.88	4.434	2.408
2	16	0.94	2.409	1.046	5	80	0.81	4.528	2.572
2	17	0.83	4.589	2.253	5	81	0.97	3.528	1.703
2	18	0.92	5.047	2.013	5	82	0.94	3.054	1.648
2	19	0.82	4.404	2.261	5	83	0.91	4.634	1.573
2	20	0.82	6.230	3.176	5	86	0.91	5.991	2.461
2	21	0.96	3.045	2.394	5	87	0.91	5.266	2.418
2	23	0.86	2.243	0.671	5	88	0.92	3.508	2.192
2	24	0.86	3.305	1.660	5	89	0.92	3.753	1.431
2	25	0.96	5.368	1.852	5	90	0.97	2.904	1.598
2	26	0.87	3.409	1.376	5	91	0.97	4.711	1.151
2	27	0.85	5.666	2.041	5	92	0.89	7.187	2.877
2	28	0.67	3.323	1.339	5	93	0.96	4.315	1.388
2	29	0.89	3.180	1.565	5	95	0.95	5.426	2.011
2	30	0.88	3.437	1.308	5	96	0.83	4.492	2.170
3	32	0.93	2.577	1.272	6	97	0.97	4.826	2.569
3	33	0.89	2.314	2.005	6	99	0.88	3.040	1.773
3	34	0.97	2.438	1.793	6	102	0.81	4.081	2.109
3	35	0.97	2.272	1.302	6	104	0.89	4.513	1.733
3	36	0.98	2.579	1.597	6	106	0.91	3.164	2.052
3	37	0.89	2.970	1.856	6	107	0.94	4.101	2.003
3	38	0.87	2.481	1.687	6	108	0.96	3.868	1.406
3	39	0.97	2.243	1.450	6	110	0.94	4.235	1.667
3	40	0.96	3.845	1.758	6	111	0.94	3.328	1.287
3	42	0.93	2.738	1.369	6	112	0.91	4.242	2.552
3	43	0.93	1.145	0.742	6	114	0.98	3.228	1.567
3	44	0.98	3.079	2.146	6	115	0.98	3.532	1.239
3	45	0.96	3.436	1.811	6	116	0.96	4.567	2.162
4	48	0.98	5.259	2.563	6	117	0.89	3.577	1.630
4	50	0.96	4.506	2.067	6	119	0.91	3.451	1.483
4	51	0.98	4.589	1.338	6	120	0.99	2.911	1.948
4	52	0.96	4.621	2.312	6	122	0.96	3.754	2.010
4	53	0.98	3.701	2.534	6	124	0.98	3.798	1.684
4	54	0.99	4.412	1.896	6	126	0.99	3.361	1.731
4	55	0.96	3.259	2.311	6	131	0.98	3.494	1.766
4	56	0.92	4.190	2.238	6	132	0.95	3.189	1.781
4	57	0.99	5.913	2.007	6	133	0.95	4.393	1.930
4	58	0.94	6.107	2.335	6	135	0.95	3.190	1.498
4	59	0.92	3.814	1.439	6	136	0.97	2.725	1.964
4	60	0.95	4.745	2.240	6	137	0.93	2.434	1.043
4	61	0.98	4.421	2.292	6	138	0.94	3.251	1.534
4	63	0.95	2.872	1.548	6	139	0.96	2.243	0.900

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 22 Family means and standard deviations (SD) for fibrous root dry weight (FROOT).[a]

Population	Family	t_m	FROOT (g)		Population	Family	t_m	FROOT (g)	
			Mean	SD				Mean	SD
1	1	0.91	1.076	0.741	4	64	0.98	0.943	0.484
1	2	0.92	1.082	0.522	4	65	0.93	1.219	0.819
1	3	0.99	0.982	0.635	4	66	0.98	1.277	0.867
1	4	0.99	1.535	0.990	4	68	0.99	1.000	0.746
1	5	0.99	0.906	0.568	4	69	0.99	0.869	0.508
1	6	0.99	1.133	0.694	4	70	0.96	1.035	0.579
1	7	0.98	1.147	0.778	4	71	0.93	0.947	0.731
1	8	0.85	1.310	0.681	5	72	0.96	1.156	0.643
1	9	0.98	0.869	0.595	5	73	0.91	1.501	0.350
1	10	0.98	0.920	0.496	5	74	0.96	2.217	1.010
1	11	0.96	0.836	0.590	5	75	0.94	1.575	0.623
1	12	0.97	0.903	0.470	5	76	0.98	2.160	0.999
1	13	0.98	1.198	0.632	5	77	0.90	1.476	0.694
1	14	0.99	1.256	0.686	5	78	0.90	1.226	0.776
1	15	0.88	1.569	0.872	5	79	0.88	1.858	0.839
2	16	0.94	1.079	0.458	5	80	0.81	1.995	1.208
2	17	0.83	1.532	0.828	5	81	0.97	1.781	0.936
2	18	0.92	1.344	0.530	5	82	0.94	1.350	0.816
2	19	0.82	0.957	0.431	5	83	0.91	2.362	0.599
2	20	0.82	2.333	1.270	5	86	0.91	2.089	0.939
2	21	0.96	0.952	0.568	5	87	0.91	1.801	0.795
2	23	0.86	1.050	0.331	5	88	0.92	1.105	0.528
2	24	0.86	1.433	0.519	5	89	0.92	1.249	0.839
2	25	0.96	1.467	0.744	5	90	0.97	1.114	0.742
2	26	0.87	0.822	0.320	5	91	0.97	1.774	0.781
2	27	0.85	1.238	0.648	5	92	0.89	1.768	1.010
2	28	0.67	0.951	0.416	5	93	0.96	1.086	0.422
2	29	0.89	0.996	0.430	5	95	0.95	2.081	0.917
2	30	0.88	1.639	0.698	5	96	0.83	1.704	0.562
3	32	0.93	1.566	0.762	6	97	0.97	1.855	0.890
3	33	0.89	1.273	0.977	6	99	0.88	1.393	0.792
3	34	0.97	1.322	0.557	6	102	0.81	1.370	0.754
3	35	0.97	1.223	0.686	6	104	0.89	1.394	0.511
3	36	0.98	1.269	0.503	6	106	0.91	1.374	0.811
3	37	0.89	1.336	0.457	6	107	0.94	1.261	0.883
3	38	0.87	1.062	0.669	6	108	0.96	1.202	0.442
3	39	0.97	0.940	0.604	6	110	0.94	1.856	0.694
3	40	0.96	1.873	0.703	6	111	0.94	1.442	0.625
3	42	0.93	1.682	0.951	6	112	0.91	1.532	0.748
3	43	0.93	1.013	0.683	6	114	0.98	1.151	0.628
3	44	0.98	1.507	0.806	6	115	0.98	0.968	0.430
3	45	0.96	1.248	0.778	6	116	0.96	1.782	0.680
4	48	0.98	1.442	0.815	6	117	0.89	1.290	0.650
4	50	0.96	1.312	0.600	6	119	0.91	1.262	0.491
4	51	0.98	1.835	0.651	6	120	0.99	0.916	0.549
4	52	0.96	1.940	0.855	6	122	0.96	1.058	0.704
4	53	0.98	1.374	0.956	6	124	0.98	1.395	0.939
4	54	0.99	1.158	0.527	6	126	0.99	0.848	0.422
4	55	0.96	0.927	0.651	6	131	0.98	1.388	0.703
4	56	0.92	1.368	0.724	6	132	0.95	1.447	0.490
4	57	0.99	1.444	0.656	6	133	0.95	1.483	0.692
4	58	0.94	1.527	0.716	6	135	0.95	1.386	0.676
4	59	0.92	1.303	0.553	6	136	0.97	1.178	0.656
4	60	0.95	1.588	0.749	6	137	0.93	0.877	0.506
4	61	0.98	1.542	0.754	6	138	0.94	1.519	0.852
4	63	0.95	1.277	0.836	6	139	0.96	1.086	0.585

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 23 Family means and standard deviations (SD) for total dry weight (TOTAL).[a]

Population	Family	t_m	TOTAL (g) Mean	SD	Population	Family	t_m	TOTAL (g) Mean	SD
1	1	0.91	8.213	4.754	4	64	0.98	9.387	5.103
1	2	0.92	7.976	3.799	4	65	0.93	10.209	6.270
1	3	0.99	8.762	3.545	4	66	0.98	10.986	4.584
1	4	0.99	10.668	4.959	4	68	0.99	9.344	5.817
1	5	0.99	6.454	3.376	4	69	0.99	9.874	5.492
1	6	0.99	9.924	3.589	4	70	0.96	11.098	5.495
1	7	0.98	9.511	4.784	4	71	0.93	10.256	5.617
1	8	0.85	9.957	5.007	5	72	0.96	9.741	3.993
1	9	0.98	7.832	4.917	5	73	0.91	14.152	3.243
1	10	0.98	7.927	4.073	5	74	0.96	18.863	5.205
1	11	0.96	6.752	3.051	5	75	0.94	16.041	6.121
1	12	0.97	8.227	3.741	5	76	0.98	16.719	6.318
1	13	0.98	9.848	4.838	5	77	0.90	12.269	5.154
1	14	0.99	8.426	4.286	5	78	0.90	12.879	7.003
1	15	0.88	10.488	4.302	5	79	0.88	16.230	7.875
2	16	0.94	6.800	2.311	5	80	0.81	13.464	7.248
2	17	0.83	11.744	5.269	5	81	0.97	13.218	6.614
2	18	0.92	11.624	3.335	5	82	0.94	11.195	6.574
2	19	0.82	10.124	4.763	5	83	0.91	18.229	4.511
2	20	0.82	17.981	7.859	5	86	0.91	19.223	6.661
2	21	0.96	8.222	5.090	5	87	0.91	15.526	5.974
2	23	0.86	7.340	2.150	5	88	0.92	10.118	4.876
2	24	0.86	9.623	3.374	5	89	0.92	11.476	4.653
2	25	0.96	13.452	3.774	5	90	0.97	10.400	4.824
2	26	0.87	8.039	2.800	5	91	0.97	14.745	4.895
2	27	0.85	13.258	3.648	5	92	0.89	18.632	7.053
2	28	0.67	8.244	2.312	5	93	0.96	11.398	3.671
2	29	0.89	7.523	3.095	5	95	0.95	17.266	5.478
2	30	0.88	10.044	3.096	5	96	0.83	15.493	5.683
3	32	0.93	9.407	3.854	6	97	0.97	14.617	7.505
3	33	0.89	8.174	4.929	6	99	0.88	10.298	5.577
3	34	0.97	9.526	4.502	6	102	0.81	12.969	4.559
3	35	0.97	8.171	3.817	6	104	0.89	12.618	5.215
3	36	0.98	9.824	4.066	6	106	0.91	10.632	7.555
3	37	0.89	9.270	3.826	6	107	0.94	13.438	6.236
3	38	0.87	8.485	4.955	6	108	0.96	11.442	3.358
3	39	0.97	6.718	3.780	6	110	0.94	15.004	8.537
3	40	0.96	13.202	5.013	6	111	0.94	12.467	4.740
3	42	0.93	11.208	3.550	6	112	0.91	15.015	7.914
3	43	0.93	6.363	3.891	6	114	0.98	10.736	3.862
3	44	0.98	11.233	6.081	6	115	0.98	10.184	3.813
3	45	0.96	11.910	5.407	6	116	0.96	14.178	5.138
4	48	0.98	12.890	5.296	6	117	0.89	10.783	4.473
4	50	0.96	12.460	4.616	6	119	0.91	9.339	3.573
4	51	0.98	16.434	4.785	6	120	0.99	8.780	5.627
4	52	0.96	17.561	7.269	6	122	0.96	10.342	5.938
4	53	0.98	11.602	6.728	6	124	0.98	10.933	4.579
4	54	0.99	11.164	3.316	6	126	0.99	9.145	4.297
4	55	0.96	8.985	5.669	6	131	0.98	9.959	4.431
4	56	0.92	11.901	5.772	6	132	0.95	10.509	3.701
4	57	0.99	15.926	5.321	6	133	0.95	13.034	4.706
4	58	0.94	15.986	6.284	6	135	0.95	9.373	3.721
4	59	0.92	11.186	2.874	6	136	0.97	8.059	4.290
4	60	0.95	13.873	6.008	6	137	0.93	7.376	2.997
4	61	0.98	14.940	5.933	6	138	0.94	11.219	3.972
4	63	0.95	10.731	6.078	6	139	0.96	7.628	3.347

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 24 Family means and standard deviations (SD) for shoot dry weight (SHOOT).[a]

Population	Family	t_m	SHOOT (g) Mean	SD	Population	Family	t_m	SHOOT (g) Mean	SD
1	1	0.91	4.487	2.467	4	64	0.98	5.866	3.337
1	2	0.92	4.124	1.751	4	65	0.93	5.917	3.805
1	3	0.99	4.786	1.831	4	66	0.98	6.741	2.600
1	4	0.99	5.002	2.181	4	68	0.99	5.921	3.671
1	5	0.99	3.306	1.806	4	69	0.99	6.054	3.490
1	6	0.99	4.673	2.141	4	70	0.96	6.162	2.427
1	7	0.98	4.327	2.107	4	71	0.93	6.772	3.390
1	8	0.85	4.763	2.531	5	72	0.96	5.430	2.037
1	9	0.98	4.123	2.806	5	73	0.91	8.022	2.440
1	10	0.98	4.246	2.178	5	74	0.96	11.079	2.746
1	11	0.96	4.294	1.991	5	75	0.94	9.020	4.204
1	12	0.97	3.947	1.870	5	76	0.98	9.134	3.548
1	13	0.98	4.959	2.385	5	77	0.90	6.502	3.076
1	14	0.99	4.399	2.739	5	78	0.90	6.797	4.349
1	15	0.88	5.134	2.232	5	79	0.88	9.938	5.082
2	16	0.94	3.312	1.223	5	80	0.81	6.942	4.232
2	17	0.83	5.623	2.543	5	81	0.97	7.909	4.655
2	18	0.92	5.233	1.593	5	82	0.94	6.790	4.618
2	19	0.82	4.763	2.422	5	83	0.91	11.234	3.118
2	20	0.82	9.419	4.330	5	86	0.91	11.143	3.884
2	21	0.96	4.225	2.339	5	87	0.91	8.460	3.272
2	23	0.86	4.048	1.400	5	88	0.92	5.506	2.696
2	24	0.86	4.885	1.702	5	89	0.92	6.474	2.776
2	25	0.96	6.617	2.218	5	90	0.97	6.383	2.921
2	26	0.87	3.808	1.863	5	91	0.97	8.260	3.342
2	27	0.85	6.354	2.112	5	92	0.89	9.677	4.108
2	28	0.67	3.970	1.297	5	93	0.96	5.998	2.476
2	29	0.89	3.408	1.353	5	95	0.95	9.759	3.237
2	30	0.88	4.968	2.000	5	96	0.83	9.297	3.873
3	32	0.93	5.265	2.415	6	97	0.97	7.937	4.517
3	33	0.89	4.666	2.551	6	99	0.88	5.865	3.321
3	34	0.97	5.766	2.702	6	102	0.81	7.518	2.904
3	35	0.97	4.677	2.150	6	104	0.89	6.710	3.407
3	36	0.98	6.060	2.563	6	106	0.91	6.094	5.027
3	37	0.89	4.965	2.125	6	107	0.94	8.077	4.075
3	38	0.87	4.942	2.759	6	108	0.96	6.372	2.446
3	39	0.97	3.534	1.959	6	110	0.94	8.913	6.800
3	40	0.96	7.484	3.276	6	111	0.94	7.697	3.255
3	42	0.93	6.788	2.047	6	112	0.91	9.241	4.987
3	43	0.93	4.205	2.785	6	114	0.98	6.357	2.476
3	44	0.98	6.647	3.377	6	115	0.98	5.684	2.341
3	45	0.96	7.226	3.421	6	116	0.96	7.829	2.879
4	48	0.98	6.189	2.413	6	117	0.89	5.916	2.495
4	50	0.96	6.643	2.397	6	119	0.91	4.705	1.934
4	51	0.98	10.010	3.865	6	120	0.99	4.953	3.472
4	52	0.96	11.000	5.214	6	122	0.96	5.531	3.556
4	53	0.98	6.526	3.565	6	124	0.98	5.741	2.521
4	54	0.99	5.594	2.295	6	126	0.99	4.936	2.587
4	55	0.96	4.798	3.102	6	131	0.98	5.077	2.250
4	56	0.92	6.429	3.247	6	132	0.95	5.873	2.269
4	57	0.99	8.568	3.400	6	133	0.95	7.158	2.628
4	58	0.94	8.352	3.988	6	135	0.95	4.798	1.798
4	59	0.92	6.068	1.547	6	136	0.97	4.155	2.086
4	60	0.95	7.539	3.552	6	137	0.93	4.065	1.819
4	61	0.98	8.978	3.367	6	138	0.94	6.449	2.190
4	63	0.95	6.582	4.166	6	139	0.96	4.299	2.229

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 25 Family means and standard deviations (SD) for root dry weight (ROOT).[a]

Population	Family	t_m	ROOT (g)		Population	Family	t_m	ROOT (g)	
			Mean	SD				Mean	SD
1	1	0.91	3.726	2.447	4	64	0.98	3.522	2.132
1	2	0.92	3.852	2.511	4	65	0.93	4.292	2.857
1	3	0.99	3.976	1.806	4	66	0.98	4.246	2.239
1	4	0.99	5.666	3.016	4	68	0.99	3.423	2.603
1	5	0.99	3.148	1.708	4	69	0.99	3.820	2.336
1	6	0.99	5.251	1.621	4	70	0.96	4.936	3.542
1	7	0.98	5.184	2.936	4	71	0.93	3.484	2.341
1	8	0.85	5.194	2.731	5	72	0.96	4.311	2.172
1	9	0.98	3.709	2.385	5	73	0.91	6.130	1.468
1	10	0.98	3.681	2.071	5	74	0.96	7.784	3.405
1	11	0.96	2.458	1.254	5	75	0.94	7.021	3.185
1	12	0.97	4.280	2.330	5	76	0.98	7.585	3.401
1	13	0.98	4.889	2.612	5	77	0.90	5.767	2.685
1	14	0.99	4.027	1.739	5	78	0.90	6.082	3.061
1	15	0.88	5.354	2.367	5	79	0.88	6.292	2.993
2	16	0.94	3.488	1.273	5	80	0.81	6.523	3.443
2	17	0.83	6.121	2.954	5	81	0.97	5.309	2.400
2	18	0.92	6.391	2.186	5	82	0.94	4.404	2.138
2	19	0.82	5.361	2.258	5	83	0.91	6.995	1.975
2	20	0.82	8.562	4.078	5	86	0.91	8.080	3.313
2	21	0.96	3.997	2.880	5	87	0.91	7.066	2.858
2	23	0.86	3.293	0.881	5	88	0.92	4.613	2.521
2	24	0.86	4.738	2.033	5	89	0.92	5.002	2.026
2	25	0.96	6.835	2.068	5	90	0.97	4.018	2.187
2	26	0.87	4.231	1.438	5	91	0.97	6.485	1.736
2	27	0.85	6.904	2.242	5	92	0.89	8.954	3.705
2	28	0.67	4.274	1.496	5	93	0.96	5.401	1.507
2	29	0.89	4.114	1.863	5	95	0.95	7.507	2.715
2	30	0.88	5.076	1.759	5	96	0.83	6.196	2.519
3	32	0.93	4.143	1.687	6	97	0.97	6.681	3.182
3	33	0.89	3.508	2.469	6	99	0.88	4.433	2.430
3	34	0.97	3.760	2.198	6	102	0.81	5.451	2.700
3	35	0.97	3.495	1.788	6	104	0.89	5.907	2.152
3	36	0.98	3.764	1.952	6	106	0.91	4.538	2.736
3	37	0.89	4.306	2.007	6	107	0.94	5.362	2.649
3	38	0.87	3.543	2.273	6	108	0.96	5.070	1.424
3	39	0.97	3.184	1.946	6	110	0.94	6.091	2.260
3	40	0.96	5.718	2.272	6	111	0.94	4.770	1.746
3	42	0.93	4.420	2.113	6	112	0.91	5.774	3.151
3	43	0.93	2.158	1.335	6	114	0.98	4.379	1.808
3	44	0.98	4.586	2.867	6	115	0.98	4.500	1.555
3	45	0.96	4.684	2.455	6	116	0.96	6.349	2.426
4	48	0.98	6.701	3.244	6	117	0.89	4.867	2.183
4	50	0.96	5.818	2.438	6	119	0.91	4.635	1.928
4	51	0.98	6.424	1.738	6	120	0.99	3.827	2.377
4	52	0.96	6.561	2.914	6	122	0.96	4.812	2.521
4	53	0.98	5.075	3.277	6	124	0.98	5.193	2.206
4	54	0.99	5.570	2.005	6	126	0.99	4.209	2.033
4	55	0.96	4.186	2.809	6	131	0.98	4.882	2.366
4	56	0.92	5.472	2.875	6	132	0.95	4.636	2.052
4	57	0.99	7.358	2.404	6	133	0.95	5.876	2.365
4	58	0.94	7.634	2.874	6	135	0.95	4.575	2.106
4	59	0.92	5.118	1.704	6	136	0.97	3.904	2.473
4	60	0.95	6.333	2.840	6	137	0.93	3.311	1.382
4	61	0.98	5.962	2.796	6	138	0.94	4.770	2.060
4	63	0.95	4.149	2.088	6	139	0.96	3.329	1.311

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 26 Family means and standard deviations (SD) for shoot to root ratio (S:R).[a]

Population	Family	t_m	S:R		Population	Family	t_m	S:R	
			Mean	SD				Mean	SD
1	1	0.91	1.40	0.65	4	64	0.98	1.97	1.04
1	2	0.92	1.31	0.69	4	65	0.93	1.44	0.56
1	3	0.99	1.34	0.42	4	66	0.98	1.91	1.06
1	4	0.99	0.94	0.29	4	68	0.99	2.23	1.35
1	5	0.99	1.11	0.26	4	69	0.99	1.73	0.79
1	6	0.99	0.87	0.26	4	70	0.96	1.68	0.89
1	7	0.98	0.97	0.49	4	71	0.93	2.15	0.71
1	8	0.85	1.02	0.43	5	72	0.96	1.50	0.83
1	9	0.98	1.34	0.59	5	73	0.91	1.34	0.41
1	10	0.98	1.48	1.09	5	74	0.96	1.63	0.63
1	11	0.96	1.89	0.65	5	75	0.94	1.50	1.06
1	12	0.97	1.09	0.62	5	76	0.98	1.30	0.42
1	13	0.98	1.09	0.35	5	77	0.90	1.23	0.70
1	14	0.99	1.09	0.28	5	78	0.90	1.15	0.51
1	15	0.88	0.99	0.29	5	79	0.88	1.76	0.90
2	16	0.94	1.00	0.28	5	80	0.81	1.15	0.36
2	17	0.83	0.95	0.23	5	81	0.97	1.50	0.55
2	18	0.92	0.87	0.28	5	82	0.94	1.51	0.35
2	19	0.82	0.93	0.33	5	83	0.91	1.67	0.48
2	20	0.82	1.17	0.38	5	86	0.91	1.51	0.50
2	21	0.96	1.21	0.48	5	87	0.91	1.24	0.30
2	23	0.86	1.23	0.29	5	88	0.92	1.35	0.50
2	24	0.86	1.10	0.39	5	89	0.92	1.30	0.29
2	25	0.96	1.01	0.34	5	90	0.97	1.92	0.93
2	26	0.87	0.91	0.40	5	91	0.97	1.26	0.27
2	27	0.85	0.98	0.40	5	92	0.89	1.18	0.51
2	28	0.67	1.02	0.37	5	93	0.96	1.12	0.38
2	29	0.89	0.90	0.27	5	95	0.95	1.35	0.40
2	30	0.88	1.01	0.42	5	96	0.83	1.62	0.86
3	32	0.93	1.27	0.48	6	97	0.97	1.17	0.33
3	33	0.89	1.58	0.63	6	99	0.88	1.44	0.54
3	34	0.97	1.64	0.73	6	102	0.81	1.57	0.67
3	35	0.97	1.53	0.66	6	104	0.89	1.13	0.39
3	36	0.98	1.81	0.86	6	106	0.91	1.25	0.44
3	37	0.89	1.19	0.32	6	107	0.94	1.79	1.09
3	38	0.87	1.62	0.64	6	108	0.96	1.28	0.44
3	39	0.97	1.17	0.45	6	110	0.94	1.39	0.62
3	40	0.96	1.37	0.42	6	111	0.94	1.67	0.48
3	42	0.93	1.85	0.98	6	112	0.91	1.69	0.47
3	43	0.93	2.11	1.03	6	114	0.98	1.73	0.88
3	44	0.98	1.64	0.49	6	115	0.98	1.24	0.20
3	45	0.96	1.75	0.76	6	116	0.96	1.26	0.23
4	48	0.98	0.99	0.24	6	117	0.89	1.24	0.27
4	50	0.96	1.26	0.44	6	119	0.91	1.07	0.35
4	51	0.98	1.61	0.60	6	120	0.99	1.37	0.62
4	52	0.96	1.91	0.89	6	122	0.96	1.20	0.38
4	53	0.98	1.39	0.32	6	124	0.98	1.16	0.35
4	54	0.99	1.12	0.72	6	126	0.99	1.28	0.45
4	55	0.96	1.43	1.10	6	131	0.98	1.25	0.66
4	56	0.92	1.33	0.58	6	132	0.95	1.38	0.56
4	57	0.99	1.19	0.33	6	133	0.95	1.26	0.29
4	58	0.94	1.16	0.43	6	135	0.95	1.14	0.38
4	59	0.92	1.33	0.66	6	136	0.97	1.26	0.69
4	60	0.95	1.26	0.62	6	137	0.93	1.27	0.53
4	61	0.98	1.66	0.46	6	138	0.94	1.50	0.54
4	63	0.95	1.63	0.49	6	139	0.96	1.31	0.39

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 27 Family means and standard deviations (SD) for specific leaf weight (SLWT).[a]

Population	Family	t_m	SLWT (g/m^2)		Population	Family	t_m	SLWT (g/m^2)	
			Mean	SD				Mean	SD
1	1	0.91	51.54	12.10	4	64	0.98	56.91	5.65
1	2	0.92	56.20	10.10	4	65	0.93	61.47	12.86
1	3	0.99	52.03	9.28	4	66	0.98	58.96	9.63
1	4	0.99	60.45	8.45	4	68	0.99	60.48	9.69
1	5	0.99	52.20	9.90	4	69	0.99	59.68	6.88
1	6	0.99	53.56	7.87	4	70	0.96	59.37	8.66
1	7	0.98	54.16	7.24	4	71	0.93	56.00	8.99
1	8	0.85	50.00	8.36	5	72	0.96	53.99	8.73
1	9	0.98	49.84	11.34	5	73	0.91	48.99	5.03
1	10	0.98	49.61	9.06	5	74	0.96	55.51	11.73
1	11	0.96	51.28	9.99	5	75	0.94	58.14	8.37
1	12	0.97	52.25	8.20	5	76	0.98	53.84	9.79
1	13	0.98	56.85	4.81	5	77	0.90	54.62	9.28
1	14	0.99	55.75	11.16	5	78	0.90	51.62	7.57
1	15	0.88	55.38	9.39	5	79	0.88	51.77	6.27
2	16	0.94	55.84	7.56	5	80	0.81	53.56	8.51
2	17	0.83	55.11	8.47	5	81	0.97	55.68	8.54
2	18	0.92	58.69	6.42	5	82	0.94	55.31	8.46
2	19	0.82	54.51	10.45	5	83	0.91	55.27	6.84
2	20	0.82	53.18	6.97	5	86	0.91	56.24	5.78
2	21	0.96	53.97	8.82	5	87	0.91	60.67	10.77
2	23	0.86	56.43	10.04	5	88	0.92	57.53	9.70
2	24	0.86	62.70	8.36	5	89	0.92	57.32	7.84
2	25	0.96	54.39	6.49	5	90	0.97	55.82	7.96
2	26	0.87	56.55	8.80	5	91	0.97	55.89	6.01
2	27	0.85	53.59	10.13	5	92	0.89	54.50	7.97
2	28	0.67	53.52	7.11	5	93	0.96	55.55	5.74
2	29	0.89	59.51	9.31	5	95	0.95	52.97	7.62
2	30	0.88	51.48	6.80	5	96	0.83	54.81	4.85
3	32	0.93	54.40	7.76	6	97	0.97	56.08	8.41
3	33	0.89	56.62	12.47	6	99	0.88	54.62	12.46
3	34	0.97	59.09	12.04	6	102	0.81	57.55	7.28
3	35	0.97	57.13	7.23	6	104	0.89	54.08	11.99
3	36	0.98	58.43	7.54	6	106	0.91	56.54	10.68
3	37	0.89	55.71	8.47	6	107	0.94	56.06	6.05
3	38	0.87	58.10	9.73	6	108	0.96	51.54	8.69
3	39	0.97	50.94	8.84	6	110	0.94	59.31	8.40
3	40	0.96	56.49	6.69	6	111	0.94	55.27	8.15
3	42	0.93	60.10	10.86	6	112	0.91	57.34	7.43
3	43	0.93	54.74	15.05	6	114	0.98	62.37	9.67
3	44	0.98	60.30	10.36	6	115	0.98	52.80	10.45
3	45	0.96	55.99	6.88	6	116	0.96	54.25	7.36
4	48	0.98	57.54	6.29	6	117	0.89	52.50	8.02
4	50	0.96	57.73	7.30	6	119	0.91	51.18	9.73
4	51	0.98	61.77	5.39	6	120	0.99	58.51	7.22
4	52	0.96	58.24	11.06	6	122	0.96	55.81	12.91
4	53	0.98	57.29	10.51	6	124	0.98	56.91	8.65
4	54	0.99	58.31	8.59	6	126	0.99	56.12	6.63
4	55	0.96	56.92	8.47	6	131	0.98	57.87	8.93
4	56	0.92	58.47	12.62	6	132	0.95	59.03	8.95
4	57	0.99	56.75	5.84	6	133	0.95	56.27	7.37
4	58	0.94	54.65	4.34	6	135	0.95	54.24	10.88
4	59	0.92	55.59	8.51	6	136	0.97	52.53	8.11
4	60	0.95	56.43	9.04	6	137	0.93	57.63	5.90
4	61	0.98	59.18	6.44	6	138	0.94	58.73	10.67
4	63	0.95	63.31	11.04	6	139	0.96	55.80	9.10

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 28 Family means and standard deviations (SD) for net photosynthesis (A, μmol m^{-2} s^{-1}).[a]

Population	Family	t_m	A		Population	Family	t_m	A	
			Mean	SD				Mean	SD
1	1	0.91	10.04	3.60	4	64	0.98	8.38	4.26
1	2	0.92	7.92	3.33	4	65	0.93	9.73	3.28
1	3	0.99	9.93	1.52	4	66	0.98	7.44	3.42
1	4	0.99	7.18	6.68	4	68	0.99	11.71	2.54
1	5	0.99	8.01	3.55	4	69	0.99	7.59	3.34
1	6	0.99	8.96	3.32	4	70	0.96	7.06	2.79
1	7	0.98	8.02	3.30	4	71	0.93	8.28	2.28
1	8	0.85	5.66	3.17	5	72	0.96	7.27	2.22
1	9	0.98	6.69	2.94	5	73	0.91	8.82	2.66
1	10	0.98	8.71	2.99	5	74	0.96	7.56	2.74
1	11	0.96	7.49	3.01	5	75	0.94	8.34	4.18
1	12	0.97	7.72	2.54	5	76	0.98	9.44	3.58
1	13	0.98	6.05	2.75	5	77	0.90	10.87	1.93
1	14	0.99	8.97	3.06	5	78	0.90	10.14	1.64
1	15	0.88	8.64	3.72	5	79	0.88	8.77	2.46
2	16	0.94	9.32	2.69	5	80	0.81	9.81	3.12
2	17	0.83	6.30	2.25	5	81	0.97	9.25	4.63
2	18	0.92	6.64	2.09	5	82	0.94	10.98	2.24
2	19	0.82	7.71	7.71	5	83	0.91	9.00	5.39
2	20	0.82	7.82	3.24	5	86	0.91	7.79	2.94
2	21	0.96	6.89	2.58	5	87	0.91	9.92	4.77
2	23	0.86	7.88	2.48	5	88	0.92	10.73	3.54
2	24	0.86	9.18	2.31	5	89	0.92	6.12	1.94
2	25	0.96	7.76	2.57	5	90	0.97	10.56	3.44
2	26	0.87	8.64	4.39	5	91	0.97	7.79	3.04
2	27	0.85	8.94	3.65	5	92	0.89	8.72	5.19
2	28	0.67	5.99	3.02	5	93	0.96	10.79	5.82
2	29	0.89	11.60	2.65	5	95	0.95	9.06	3.69
2	30	0.88	6.41	3.30	5	96	0.83	8.22	3.97
3	32	0.93	5.97	2.81	6	97	0.97	10.70	4.52
3	33	0.89	5.31	3.16	6	99	0.88	7.87	2.38
3	34	0.97	9.47	4.32	6	102	0.81	10.45	3.04
3	35	0.97	8.64	3.62	6	104	0.89	10.75	2.79
3	36	0.98	8.60	3.99	6	106	0.91	8.45	4.05
3	37	0.89	7.67	4.14	6	107	0.94	5.15	2.32
3	38	0.87	10.68	3.00	6	108	0.96	8.52	2.66
3	39	0.97	9.45	4.46	6	110	0.94	9.10	4.47
3	40	0.96	8.83	5.38	6	111	0.94	8.54	2.10
3	42	0.93	7.31	3.72	6	112	0.91	6.38	1.92
3	43	0.93	5.70	4.24	6	114	0.98	8.86	4.02
3	44	0.98	5.66	3.12	6	115	0.98	6.05	2.06
3	45	0.96	9.14	5.28	6	116	0.96	9.38	2.91
4	48	0.98	7.72	3.99	6	117	0.89	8.49	2.54
4	50	0.96	11.33	2.17	6	119	0.91	11.06	2.94
4	51	0.98	10.54	2.64	6	120	0.99	7.63	3.51
4	52	0.96	6.29	2.92	6	122	0.96	8.65	2.78
4	53	0.98	7.91	1.51	6	124	0.98	9.58	2.00
4	54	0.99	6.86	1.27	6	126	0.99	9.42	3.95
4	55	0.96	9.12	2.65	6	131	0.98	7.78	3.41
4	56	0.92	10.68	5.90	6	132	0.95	7.22	2.61
4	57	0.99	8.05	2.64	6	133	0.95	5.94	2.57
4	58	0.94	7.19	1.24	6	135	0.95	10.75	3.44
4	59	0.92	9.64	1.53	6	136	0.97	6.85	2.48
4	60	0.95	8.42	1.77	6	137	0.93	7.63	2.68
4	61	0.98	7.14	3.14	6	138	0.94	7.94	2.56
4	63	0.95	8.35	2.49	6	139	0.96	7.72	4.05

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 29 Family means and standard deviations (SD) for transpiration (E, mmol m^{-2} s^{-1}).[a]

Population	Family	t_m	E		Population	Family	t_m	E	
			Mean	SD				Mean	SD
1	1	0.91	1.44	0.33	4	64	0.98	1.77	1.12
1	2	0.92	1.31	0.72	4	65	0.93	1.63	0.63
1	3	0.99	2.18	0.56	4	66	0.98	1.15	0.53
1	4	0.99	1.52	1.42	4	68	0.99	1.84	0.71
1	5	0.99	1.82	1.13	4	69	0.99	1.23	0.36
1	6	0.99	1.73	0.78	4	70	0.96	1.16	0.52
1	7	0.98	1.69	0.83	4	71	0.93	1.23	0.37
1	8	0.85	1.35	0.69	5	72	0.96	1.18	0.41
1	9	0.98	1.32	0.62	5	73	0.91	1.60	0.67
1	10	0.98	1.18	0.41	5	74	0.96	1.17	0.46
1	11	0.96	1.13	0.31	5	75	0.94	1.08	0.63
1	12	0.97	1.19	0.42	5	76	0.98	1.62	0.72
1	13	0.98	1.14	0.40	5	77	0.90	1.48	0.48
1	14	0.99	1.78	0.81	5	78	0.90	1.46	0.40
1	15	0.88	1.59	0.64	5	79	0.88	1.20	0.28
2	16	0.94	1.71	0.54	5	80	0.81	1.39	0.62
2	17	0.83	1.39	0.72	5	81	0.97	1.30	0.67
2	18	0.92	1.09	0.38	5	82	0.94	1.51	0.56
2	19	0.82	1.45	0.88	5	83	0.91	1.25	0.80
2	20	0.82	1.13	0.41	5	86	0.91	1.18	0.47
2	21	0.96	1.25	0.93	5	87	0.91	1.63	1.10
2	23	0.86	1.36	0.49	5	88	0.92	1.74	0.63
2	24	0.86	1.68	0.52	5	89	0.92	0.98	0.24
2	25	0.96	1.30	0.55	5	90	0.97	1.48	0.55
2	26	0.87	1.29	0.71	5	91	0.97	1.18	0.50
2	27	0.85	1.51	0.64	5	92	0.89	1.05	0.31
2	28	0.67	1.25	0.84	5	93	0.96	1.90	1.14
2	29	0.89	1.96	0.67	5	95	0.95	1.31	0.37
2	30	0.88	1.11	0.37	5	96	0.83	1.00	0.56
3	32	0.93	0.97	0.51	6	97	0.97	1.62	0.53
3	33	0.89	1.05	0.49	6	99	0.88	1.06	0.47
3	34	0.97	1.19	0.59	6	102	0.81	2.08	0.68
3	35	0.97	1.34	0.52	6	104	0.89	1.54	0.47
3	36	0.98	1.68	0.87	6	106	0.91	1.43	0.59
3	37	0.89	1.34	0.69	6	107	0.94	1.22	0.87
3	38	0.87	1.86	0.84	6	108	0.96	1.59	0.81
3	39	0.97	1.65	0.89	6	110	0.94	1.52	0.96
3	40	0.96	1.42	0.75	6	111	0.94	1.49	0.53
3	42	0.93	1.19	0.70	6	112	0.91	0.91	0.44
3	43	0.93	0.89	0.54	6	114	0.98	1.29	0.29
3	44	0.98	1.06	0.75	6	115	0.98	0.97	0.31
3	45	0.96	1.40	0.81	6	116	0.96	1.72	0.88
4	48	0.98	1.27	0.66	6	117	0.89	1.29	0.58
4	50	0.96	2.03	0.48	6	119	0.91	2.48	0.74
4	51	0.98	1.52	0.36	6	120	0.99	1.19	0.50
4	52	0.96	1.03	0.41	6	122	0.96	1.20	0.54
4	53	0.98	1.28	0.34	6	124	0.98	1.46	0.69
4	54	0.99	1.33	0.50	6	126	0.99	1.36	0.70
4	55	0.96	1.70	0.48	6	131	0.98	1.44	0.73
4	56	0.92	1.81	0.89	6	132	0.95	1.31	0.62
4	57	0.99	1.07	0.51	6	133	0.95	1.19	0.71
4	58	0.94	1.35	0.51	6	135	0.95	2.02	1.20
4	59	0.92	1.59	0.38	6	136	0.97	1.44	0.73
4	60	0.95	1.37	0.66	6	137	0.93	1.34	0.47
4	61	0.98	1.21	0.69	6	138	0.94	1.35	0.50
4	63	0.95	0.99	0.33	6	139	0.96	1.60	1.27

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).

Appendix 30 Family means and standard deviations (SD) for water-use efficiency (WUE, μmol CO_2 /mmol H_2O).[a]

Population	Family	t_m	WUE		Population	Family	t_m	WUE	
			Mean	SD				Mean	SD
1	1	0.91	7.50	3.87	4	64	0.98	5.28	1.82
1	2	0.92	6.46	1.96	4	65	0.93	6.63	2.64
1	3	0.99	4.75	1.03	4	66	0.98	6.45	1.50
1	4	0.99	5.10	1.88	4	68	0.99	7.09	2.44
1	5	0.99	5.30	2.19	4	69	0.99	6.03	1.80
1	6	0.99	5.74	2.44	4	70	0.96	6.40	1.55
1	7	0.98	5.10	1.62	4	71	0.93	7.15	2.50
1	8	0.85	4.32	1.77	5	72	0.96	6.40	1.57
1	9	0.98	5.68	2.36	5	73	0.91	6.08	1.98
1	10	0.98	7.78	2.98	5	74	0.96	6.69	1.49
1	11	0.96	6.49	1.49	5	75	0.94	8.26	2.27
1	12	0.97	6.74	1.62	5	76	0.98	6.03	0.66
1	13	0.98	5.28	1.91	5	77	0.90	8.00	2.74
1	14	0.99	5.62	2.14	5	78	0.90	7.44	2.55
1	15	0.88	5.55	3.01	5	79	0.88	7.38	1.75
2	16	0.94	6.18	3.11	5	80	0.81	8.03	2.87
2	17	0.83	5.34	2.53	5	81	0.97	7.26	2.51
2	18	0.92	6.36	1.95	5	82	0.94	8.41	3.86
2	19	0.82	6.45	2.62	5	83	0.91	8.86	4.17
2	20	0.82	6.83	1.04	5	86	0.91	6.86	1.22
2	21	0.96	7.20	3.12	5	87	0.91	6.90	2.20
2	23	0.86	6.35	3.11	5	88	0.92	6.55	2.29
2	24	0.86	5.78	1.94	5	89	0.92	6.26	1.61
2	25	0.96	6.33	1.55	5	90	0.97	7.59	2.63
2	26	0.87	7.15	1.92	5	91	0.97	7.27	2.54
2	27	0.85	6.39	2.60	5	92	0.89	8.28	3.52
2	28	0.67	5.34	1.60	5	93	0.96	6.21	3.07
2	29	0.89	6.30	1.78	5	95	0.95	6.99	2.48
2	30	0.88	5.52	1.94	5	96	0.83	8.59	1.80
3	32	0.93	6.45	1.58	6	97	0.97	6.91	2.81
3	33	0.89	4.95	1.89	6	99	0.88	7.97	2.08
3	34	0.97	8.40	3.29	6	102	0.81	5.40	2.15
3	35	0.97	7.03	3.18	6	104	0.89	7.36	2.15
3	36	0.98	6.06	4.19	6	106	0.91	6.28	2.05
3	37	0.89	5.79	3.04	6	107	0.94	5.41	2.56
3	38	0.87	6.60	3.33	6	108	0.96	6.24	2.73
3	39	0.97	6.38	3.81	6	110	0.94	6.41	2.28
3	40	0.96	6.02	2.59	6	111	0.94	6.52	2.74
3	42	0.93	6.23	1.69	6	112	0.91	7.55	1.96
3	43	0.93	6.78	3.41	6	114	0.98	6.69	1.89
3	44	0.98	6.24	3.56	6	115	0.98	6.32	1.73
3	45	0.96	6.90	2.83	6	116	0.96	6.09	2.03
4	48	0.98	5.97	1.25	6	117	0.89	7.80	3.75
4	50	0.96	5.70	0.98	6	119	0.91	4.86	2.02
4	51	0.98	7.10	1.65	6	120	0.99	6.71	2.51
4	52	0.96	6.04	0.78	6	122	0.96	8.20	3.02
4	53	0.98	6.86	3.42	6	124	0.98	8.04	4.00
4	54	0.99	5.61	1.72	6	126	0.99	7.36	1.68
4	55	0.96	5.46	1.44	6	131	0.98	6.09	2.94
4	56	0.92	6.02	2.58	6	132	0.95	6.30	2.98
4	57	0.99	8.83	3.69	6	133	0.95	5.41	1.23
4	58	0.94	6.19	3.23	6	135	0.95	6.44	2.26
4	59	0.92	6.43	2.22	6	136	0.97	5.46	2.36
4	60	0.95	7.25	3.13	6	137	0.93	6.01	1.87
4	61	0.98	6.36	1.47	6	138	0.94	6.15	1.69
4	63	0.95	9.31	4.06	6	139	0.96	6.12	4.63

[a] t_m indicates estimates of multilocus outcrossing rate using isozyme data (Chapter 3).